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UNIVERSITY OF ALBERTA

ECOLOGY OF A NORTHERN POPULATION OF THE RED SQUIRREL,

Tamiasciurus hudsonicus preblei (Howell)

by

© David L. Zirul

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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Thesis

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Ecology of a northern population of the red squirrel, *Tamiasciurus hudsonicus preblei* (Howell)" submitted by David L. Zirul in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

A population of red squirrels (*Tamiasciurus hudsonicus preblei*) near Great Slave Lake, Northwest Territories, Canada was studied during 14 months from July 1968 through August 1969. Autopsy data on 300 squirrels, and a live-trapping record of 53 others on a 31.25 acre study plot, were examined and compared with the results of previous works on more southern subspecies. Emphasis throughout the study was on responses to the long, cold winters and brief summers of the north, especially those adaptive phenomena which do not appear at lower latitudes.

Northern red squirrels were found to be larger than their southern relatives - in keeping with Bergmann's rule. Metabolic adaptations to cold stress were also recorded, notably the presence of a yearly cycle in brown fat weight.

A more intense territoriality was noted for northern squirrels than described for more southern subspecies, apparently acting to increase the stability of the population. The importance of "communal food stores" in such a population is discussed.

Anal gland weights showed seasonal variations with apparent population density. Function of these organs as scent glands for territory marking is discussed.

The growth rate in northern squirrels is apparently faster than for those in the south. This relationship is apparently of importance in taking advantage of the short northern summer.

Maternal behavior seemed to favor the establishment, and therefore the survival, of female young over their male littermates. The

significance of this in a species in which males are promiscuous is discussed.

Squirrels in the north are shorter lived and less fecund than those at lower latitudes. Therefore, the significance of an abundance of females to raise the reproductive potential of the population is increased. Metabolic and behavioral sources of increased mortality in adult males, with special emphasis on those during the spring critical period, are discussed. The increased reproduction achieved by these forces, however, seemed relatively minor. In order to offset higher mortality rates in northern populations, a significantly increased natality rate was expected. This is apparently effected by an increase in the percentage of breeders in the female cohort of more northern populations.

ACKNOWLEDGEMENTS

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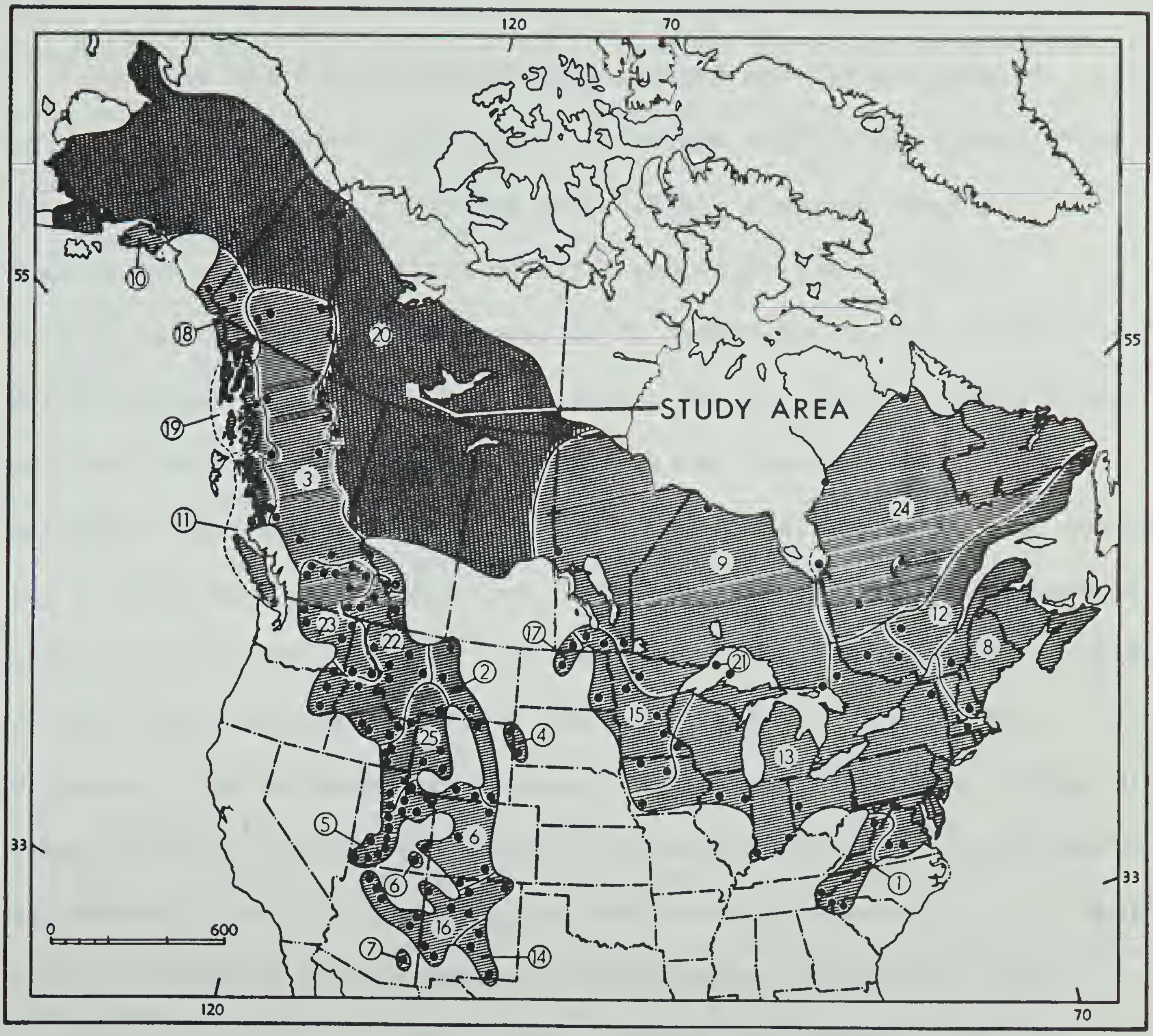
INTRODUCTION

Tamiasciurus hudsonicus is a common diurnal rodent of coniferous forests of North America, found also in many deciduous forests of Canada and the northeastern United States where not out-competed by squirrels of the genus *Sciurus* (Figure 1). Although a furbearer of some economic importance, there has been until recently a paucity of information on its biology. The purpose of this study was to investigate aspects of the biology of *T. h. preblei* (Howell) for which published information is lacking. The study was divided to conduct inquiry along two rather broad lines:

I. to yield information on the general biology of the subspecies through the collection of specimens for autopsy

II. to yield information on the ecology of a local population of red squirrels through an intensive capture-recapture program in an area characteristic of one common boreal forest plant association

As *T. h. preblei* is the most northern subspecies of its genus, and the study was conducted in the Northwest Territories, Canada, special attention was given to effects of the most striking environmental factor: climate. It was hoped that the study would reveal responses to climate previously unrecorded for Sciuridae, at least outside of the Russian literature. Knowledge of such responses could yield valuable insight into the biology of species in temperate regions as well, where similar responses may be important but not as readily apparent to the investigator.



Map 257. *Tamiasciurus hudsonicus.*

Guide to subspecies
1. *T. h. abieticola*
2. *T. h. baileyi*
3. *T. h. columbiensis*
4. *T. h. dakotensis*
5. *T. h. dixiensis*
6. *T. h. fremonti*
7. *T. h. grahamensis*
8. *T. h. gymnicus*
9. *T. h. hudsonicus*
10. *T. h. kenaiensis*
11. *T. h. lanuginosus*
12. *T. h. laurentianus*
13. *T. h. loquax*
14. *T. h. lychnuchus*
15. *T. h. minnesota*
16. *T. h. mogollonensis*
17. *T. h. pallescens*
18. *T. h. petulans*
19. *T. h. picatus*
20. *T. h. preblei*
21. *T. h. regalis*
22. *T. h. richardsoni*
23. *T. h. streatori*
24. *T. h. ungavensis*
25. *T. h. ventorum*

FIGURE 1 . GEOGRAPHIC RANGE OF THE RED SQUIRREL WITH THE RANGE OF T. h. preblei EMPHASIZED AND STUDY AREA INDICATED.(MODIFIED FROM HALL AND KELSON, 1959)

LITERATURE REVIEW

Works of the 19th and early 20th century were in the form of general surveys (Seton 1909, 1929), or essays with little quantitative data. Works of Klugh (1927) and Hatt (1929), although largely descriptive, formed the first detailed and objective accounts of ecology, life history and behavior of *T. hudsonicus* in the northeastern United States. Hamilton's (1939) account of red squirrel life history was the first set down in quantitative terms. Layne (1952, 1954) described the vestigial nature of the *os genitale*, and dealt with ecology and life history of *T. hudsonicus* in New York - the first comprehensive modern works on this species. Kilham's (1954) work on behavior of this animal in the New England States was the last for 10 years. Then Halvorson (1964 to 1966), in a series of unpublished reports discussed census methods, marking techniques, food habits and population density-dependence of red squirrels on pine cone crops in Colorado. C. C. Smith (1965) stimulated renewed interest in the genus *Tamiasciurus* with a comprehensive thesis on interactions between red squirrels and the Douglas squirrel (*T. douglasii*) in southern British Columbia. (Smith's (1968) first publication was on the adaptive nature of social organization within the genus.) Brink (1964), Brink and Dean (1966), and M. C. Smith (1967) conducted studies on the dependence of red squirrels on spruce seed in interior Alaska. The study closest to the region chosen for this program was completed by Wood (1967), which consisted of a general picture of ecology and population dynamics of the red squirrel in Wood Buffalo National Park. Following Wood's (1967) thesis, two more have been completed: Millar (1968) on reproductive biology in southern

British Columbia, and Krasnowski (1969) on population structure and breeding biology in Interior Alaska. Studies by Rusch, Reeder and Kemp on red squirrel ecology in the boreal forest at Rochester, Alberta, are as yet unavailable.

Much of the literature useful to a study being conducted on *Tamiasciurus* has been published on the closely related genus *Sciurus*, mainly on the grey (*S. carolinensis*) and fox (*S. niger*) squirrels of the deciduous forest regions of the United States (introduced in Great Britain and Stanley Park, Vancouver, British Columbia). Most studies of these species are concerned with their management as game animals, but some are more widely useful: Allanson (1933) on the reproductive biology of the male grey squirrel, Deansley and Parkes (1933) on that of the female, Kirkpatrick (1955) on the testes of the fox squirrel, and Flyger (1955, 1960) on social behavior and home range of the grey squirrel. Further, a wealth of Russian and Finnish literature on the Eurasian red squirrel, *Sciurus vulgaris*, is available to those who can read these languages, but little has been translated into English. Notable exceptions are contained in Ognev's (1940) Mammals of the USSR Vol. 4, and Lampio's (1965, 1967) works on sex ratios.

THE STUDY AREA

I. General

The study area was a strip of land about 2 miles wide and 30 miles long, from mileposts 66 to 96 along the Mackenzie Highway (N.W.T. 1). The base of operations was the Heart Lake Biological Station of the University of Alberta, at milepost 81.6 (60°50'N., 116°35'W.). This region is about eight miles southwest of Great Slave Lake, in the Northwest Territories, Canada. Elevation varies from 750 to 850 feet above sea level.

Three major vegetation types were recognized. In decreasing order of total area of cover these are:

Forests of mixed jackpine (*Pinus banksiana*) and white spruce (*Picea glauca*) cover regions of well drained gravel soils, with climax white spruce stands usually prevented by fire. Poplar (*Populus tremuloides*) is common. Tree size averages 20-40 feet in height and 4-8 inches d.b.h., with larger trees up to 80 feet and 24 inches d.b.h. in rare stands approaching climax. Understory vegetation is varied, depending usually on stand age (humus depth, shade, and humidity). The change in the understory with age is from bearberry (*Arctostaphylos uva-ursi*) and some common juniper (*Juniperus communis*) in the newer areas; through prostrate juniper (*Juniperus horizontalis*), alder (*Alnus crispa*), bog cranberry (*Vaccinium vitis-idaea*), reindeer moss (*Cladonia* sp.) and often dense clumps of raspberry (*Rubus strigosus*) in slightly older areas; to a primarily feather moss (*Hylocomium splendens*) floor with some high-bush cranberry (*Viburnum edule*) in the areas approaching climax. This zone may be split

into three distinct landscape types using these criteria. A fourth results when limestone bedrock is at the surface, causing extremely dry conditions - grassy clearings with much *Juniperus communis* and fewer, scattered trees.

Areas of black spruce (*Picea mariana*) and tamarack (*Larix laricina*) are the second most common and cover most poorly drained regions of the boreal forest. Understory vegetation is primarily birch (*Betula glandulosa*) and *Sphagnum*.

The third vegetation type is comprised mainly of small jackpine (less than 12 feet in height, 3 inches d.b.h.). As a fire succession stage this usually leads to a white spruce-jackpine association. Understory vegetation is usually of grasses.

II. Live-Trapping Plot

A study plot for live-trapping studies was set out in the mixed jackpine-white spruce forest near the field station. It encompassed 31.25 acres - a rectangle 100 rods by 50 rods with its long axis lying north-south magnetic. The areas covered by each of the four landscape types described for this vegetation type were approximately: 5.10 acres open dry, 11.50 acres semi-open dry, 7.07 acres semi-open wet and 7.58 acres of the dense wet type (Figure 2). Table 1 presents the results of plant composition surveys for these four divisions. Figure 3 shows representative samples of each landscape type.

Maximum and minimum temperatures were recorded daily from September 1968 to September 1969. Temperatures were taken from a Taylor thermometer in the Mackenzie Forest Service's Stevenson screen, set at breast height in a small clearing about 200 feet north-west of the study plot. Ten-day "means" of these values were calculated to show gross changes in

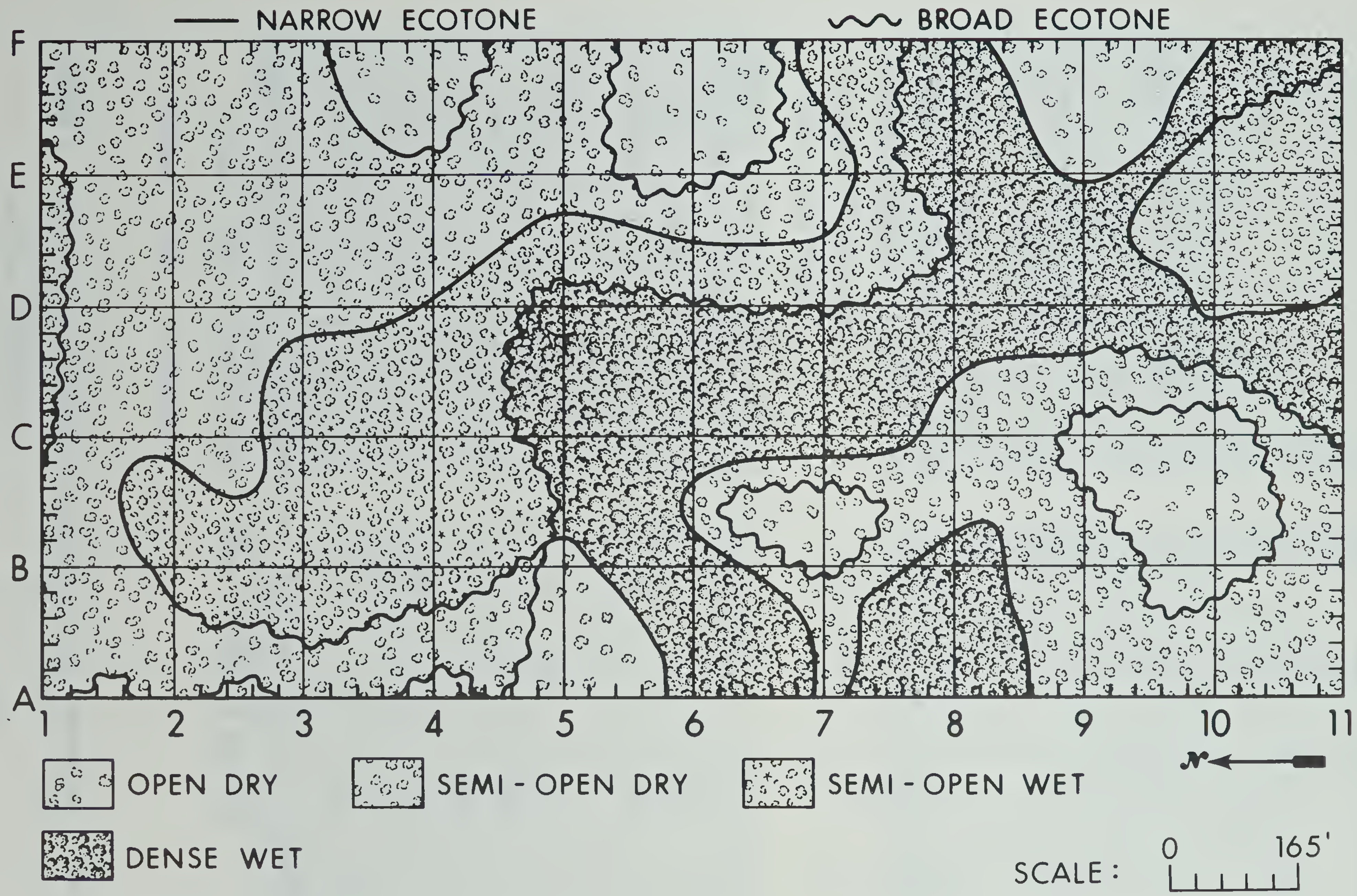


FIGURE 2. STUDY PLOT - LANDSCAPE TYPE

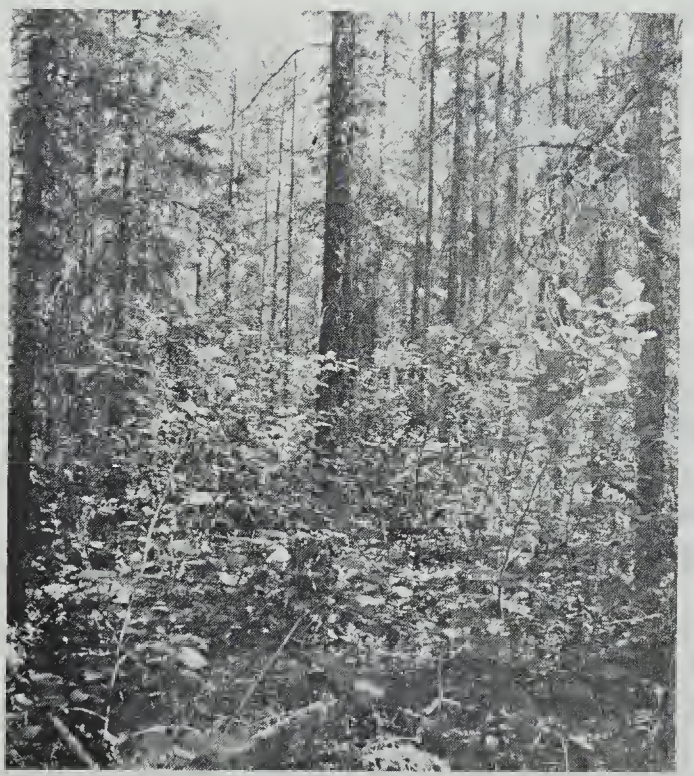
	Open dry	Semi-open dry	Semi-open wet	Dense wet
Acreage	5.10	11.50	7.07	7.58
Trees per acre	14	240	340	610
Pinus banksiana av. height	40'	45'	50'	40'
av. d.b.h.	10"	5.5"	8.5"	4.5"
Picea glauca av. height	4-70'	60'	70'	30'
av d.b.h.	1-10"	7.5"	9"	3.5"
Relative density - tree level:				
Pinus banksiana	10%	70%	55%	27%
Picea glauca	76%	27%	40%	73%
Populus tremuloides	13%	2%	5%	0
Betula papyrifera	1%	1%	0	0
Relative density - shrub level:				
Juniperus communis	100%	90%	0	0
Alnus crispa	0	9%	85%	0
Viburnum edule	0	1%	15%	0
Relative density - herb level:				
Arctostaphylos uva-ursi	12%	80%	10%	0
Juniperus horizontalis	0	8%	20%	0
Vaccinium vitis-idaea	0	0	10%	2%
Elymus innovatus	88%	2%	2%	0
Cladonia sp.	0	8%	30%	0
Hylocomium splendens	0	2%	28%	98%

Common also in local situations are: *Rosa acicularis*, *Geocaulon lividum*, *Ribes oxyacanthoides*, *Rubus strigosus* and the foliose lichen, *Peltigera* sp.

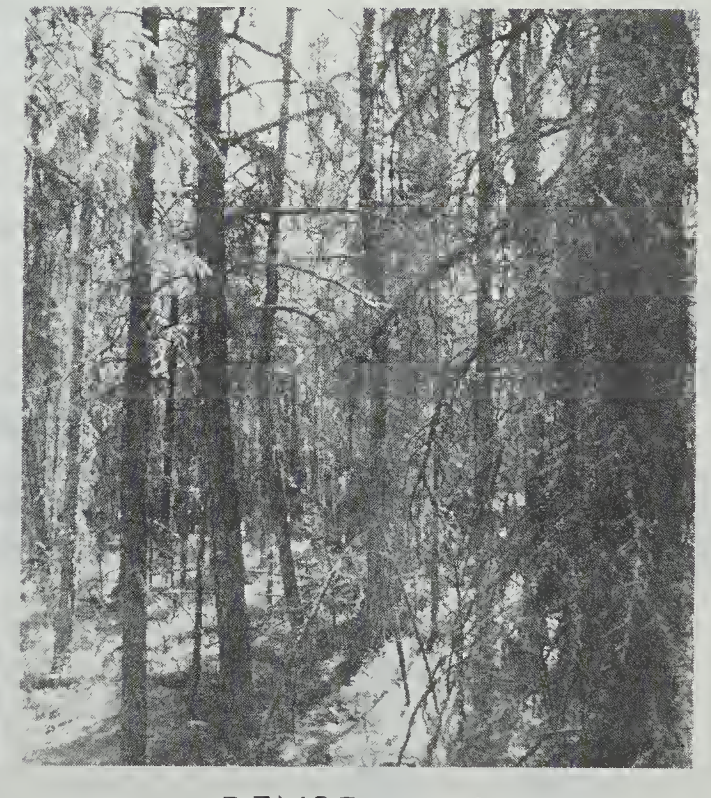
TABLE 1. Cover relationships between the four landscape types on the study plot.

OPEN DRY

SEMI-OPEN DRY



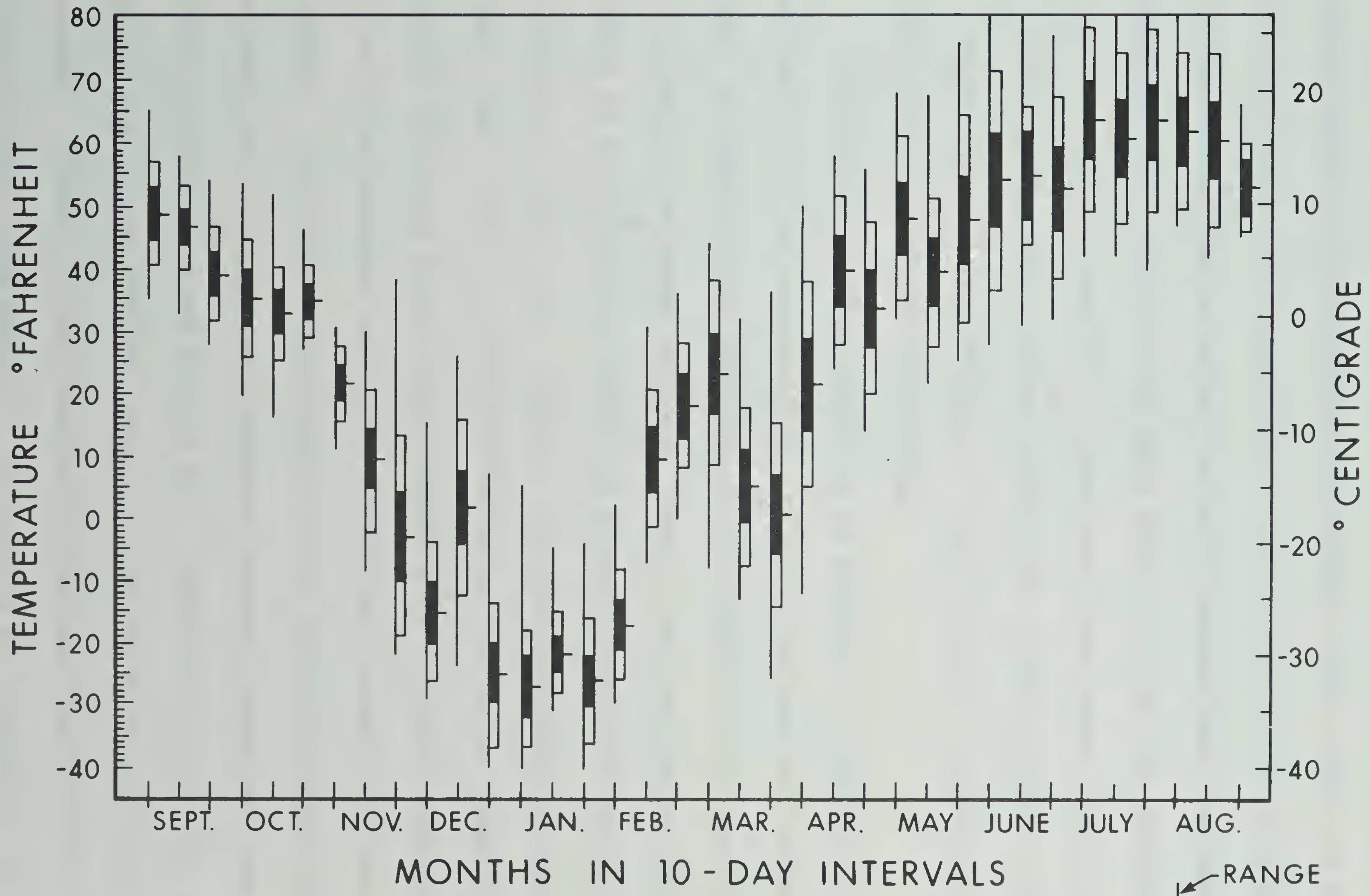
SEMI-OPEN WET



DENSE WET

FIGURE 3 .APPEARANCE OF EACH OF THE LANDSCAPE TYPES ON THE RED SQUIRREL LIVE-TRAPPING PLOT



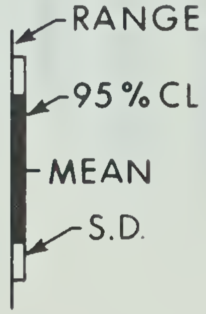


FIGURE 4. TEMPERATURE DATA STATISTICALLY TREATED IN 10-DAY INTERVALS SEPT. 1968 TO SEPT. 1969

temperature range during the study period (Figure 4). Temperatures averaged below freezing from November to early April, below 0°F. from late November to early February, and below -20°F. from late December through January. The temperature decline in fall was quite regular, but the spring warming period was not. Temperatures approached melting in late February and early March, but for the remainder of March the mean was near 0°F. There was a very sharp rise in temperature in early April, when daytime temperatures usually ranged to 40°F. and at night dropped below freezing. From mid-April through May temperatures usually stayed well above freezing.

The first permanent snow fell on October 28, 1968 and by March had built up to approximately 20 inches in the open dry landscape type, 16 inches in the semi-open dry, 14 inches in the semi-open wet and 10 inches in the dense wet type. Snow in the more dense landscapes tended to be lighter and less deep because of snow collecting on the branches of trees (qali - Pruitt 1958) than the dense, crusted snows of open areas. This was reflected in the way the snows disappeared in spring, with bare ground first appearing in the dense landscape types in April but unbroken snow cover persisting through early May in open regions. Due to the rapid spring melt of 1969 much of the forest floor of semi-open and dense wet landscapes became flooded with near-freezing water through April and most of May. Weather data for Heart Lake during spring and summer 1968 were obtained from the Mackenzie Forest Service records. "Means" of daily maximum and minimum temperatures in two-week intervals were, from March 1: 10, 18, 21, not available, 38, 44, 46, 55, 55, 56, 52 and 53°F. to the end of August. Snow persisted much later in the spring of 1968 than in 1969, and new snow was recorded as

late as May 15. Precipitation was apparently much greater in the second summer, with 22 days of rain recorded from June to August of 1968 and 46 days of rain during the same period in 1969. The persistance of snow and ground water and the warmer, drier summer of 1968 created a much better berry season than the sudden melt and cool, wet summer of 1969.

METHODS

I. General Biology

a. Collection

A number of methods of collecting specimens for autopsy were tested. The final choice, as the only way to ensure a fresh and relatively undamaged specimen, was a .22 rifle. Other items tested were shotguns of various gauges and chokes, snares using different wire types, Oneida-Victor steel traps, and National live-traps. In coldest weather when squirrel activity was minimal, the supplementary methods chosen as best of their type were: a 16 ga. shotgun with open bore and #6 shot, snares of #22 brass wire, Oneida-Victor #1 1/2 steel traps, and National live-traps. The disadvantages of these were their tendency to yield shot-damaged or starved and frozen specimens. The most useful were the #1 1/2 steel traps (large, as an animal caught by one foot would often escape through freezing and wringing off of the appendage), set in a snow tunnel near a center of squirrel activity.

b. Autopsy

In each autopsy, total weight was recorded, and also in sequence: condition of the cased skin, standard external measurements, anal gland weight, axillary brown fat weight, reproductive tract data (Male; testes length, width, weight, position and appearance, prostate length and width, size of epididymides and seminal visicles and the presence or absence of sperm in smears taken from testes, epididymides and seminal vesicles. Female; size and condition of nipples and mammary glands, length and width of ovaries and uterine cornua, counts of

corpora lutea, counts of placental scars or length, weight and condition of embryos when present, presence or absence of sperm, leucocytes or desquamated cells in vaginal smears, and width and appearance of the vagina), weights of liver, kidneys, adrenals, and spleen in milligrams per gram of body weight, weight of the stomach (with analysis of contents) greatest length and zygomatic breadth of skull, length of mid-sagittal crest suture, length of dentary from condyle to tip of the incisor, condition of teeth, crown length of upper cheek tooth row, length of femur from greater trochanter to lateral epicondyle, and degree of epiphyseal closure in the femur. Collected were: skins, skulls, dentary bones, femur, (dried); stomachs (in AFA); reproductive tracts (in Bouin's to 70% Ethanol after 7 days) and parasites (in 70% Ethanol). Numerical data were separated by age, sex and season and were examined statistically for mean, standard error and standard deviation of the mean. Standard error was the estimate of variability used for means given in the text, but was converted to 95 per cent confidence limits in figures. Only normal specimens, autopsied while still fresh, were included in these samples. All data were arranged to show temporal and sexual differences graphically, and wherever necessary exact values were also given in the text.

All samples and records from autopsy studies, whether or not examined in this thesis, have been deposited in the University of Alberta Museum of Zoology.

II. Ecology of a Local Population

a. Live-trapping

The study plot was surveyed as a grid with six rows A to F and lines 1 to 11, each spaced 10 rods apart (Figure 2). A National live-trap was placed in a protected spot at each intersection. Alternate rows were trapped each day to minimize interference with natural squirrel movements. Traps were left open only during daylight hours to eliminate overnight exposure of squirrels and to prevent excessive capture of nocturnal animals. Traps were checked twice daily during short winter days and thrice between dawn and dusk in summer.

Food (Purina Rat Chow) was kept in the traps, not as a bait, but to ensure that squirrels would not suffer from starvation shock, especially in extreme cold. As squirrels were curious and would investigate an open trap, bait *per se* was unnecessary.

A quantity of bedding (terylene fiber) was always present in traps and was most important during cold periods as an insulative material. Terylene was preferred to cotton as it is non-absorbant. This advantage outweighed the tendency of long-fiber terylene to occasionally entangle captured animals and harm them before release.

All traps were wrapped in 6-mil black plastic. This created a dark refuge where a captured animal would rest rather than struggle into terminal shock. Other advantages were: during cold weather the black cover tends to absorb any heat from the weak winter sun, or if covered with snow there is insulation from the outside. The plastic also gives shelter, in preventing rain or snow from entering the trap.

Handling of captured animals involved marking on first capture, and recording body weights periodically thereafter. Marking was by the

toe-clipping method. Other marking methods, using color-coded wire loops, metal tags or pelage clipping, were avoided as potentially harmful to the animal. The sequence chosen for toe-clipping used the front digits as numbers 1 to 8 and the hind digits as 10 to 100, numbered from left to right in dorsal aspect (The unit 9 could not be used).

To handle captured animals, modifications of Emlen's (1944) wire cone (Figure 5) and a canvas sock were used. This method presented least chance of injury to the animal or the handler. The canvas sock was held secure over a trap entrance by a length of shock cord. A plastic window sewn in the closed end facilitated squirrel entrance. This sock was used for weighing, and if marking was necessary the animal could be transferred to the wire cone to be held. Anaesthetic was not used as it was deemed unnecessary, time consuming, and dangerous to the animal.

b. Calculation of home range

For calculation of home range a variation of the "boundary strip" method was used. Initially a minimum area was enclosed. This was followed by the addition of a boundary strip varying in width with the number of times a particular squirrel was captured at each boundary trap. The distance between traps (10 rods) was split into 5 capture-intervals of 2 rods each. For every recapture at a boundary trap, the animal was considered to have moved one 2-rod interval beyond it. If an animal was captured more than four times at a trap, and yet did not reach the next, the animal was considered to have moved 9 rods from the boundary recapture. Single captures well outside of normal ranges were treated as sporadic movements and mapped as narrow lines

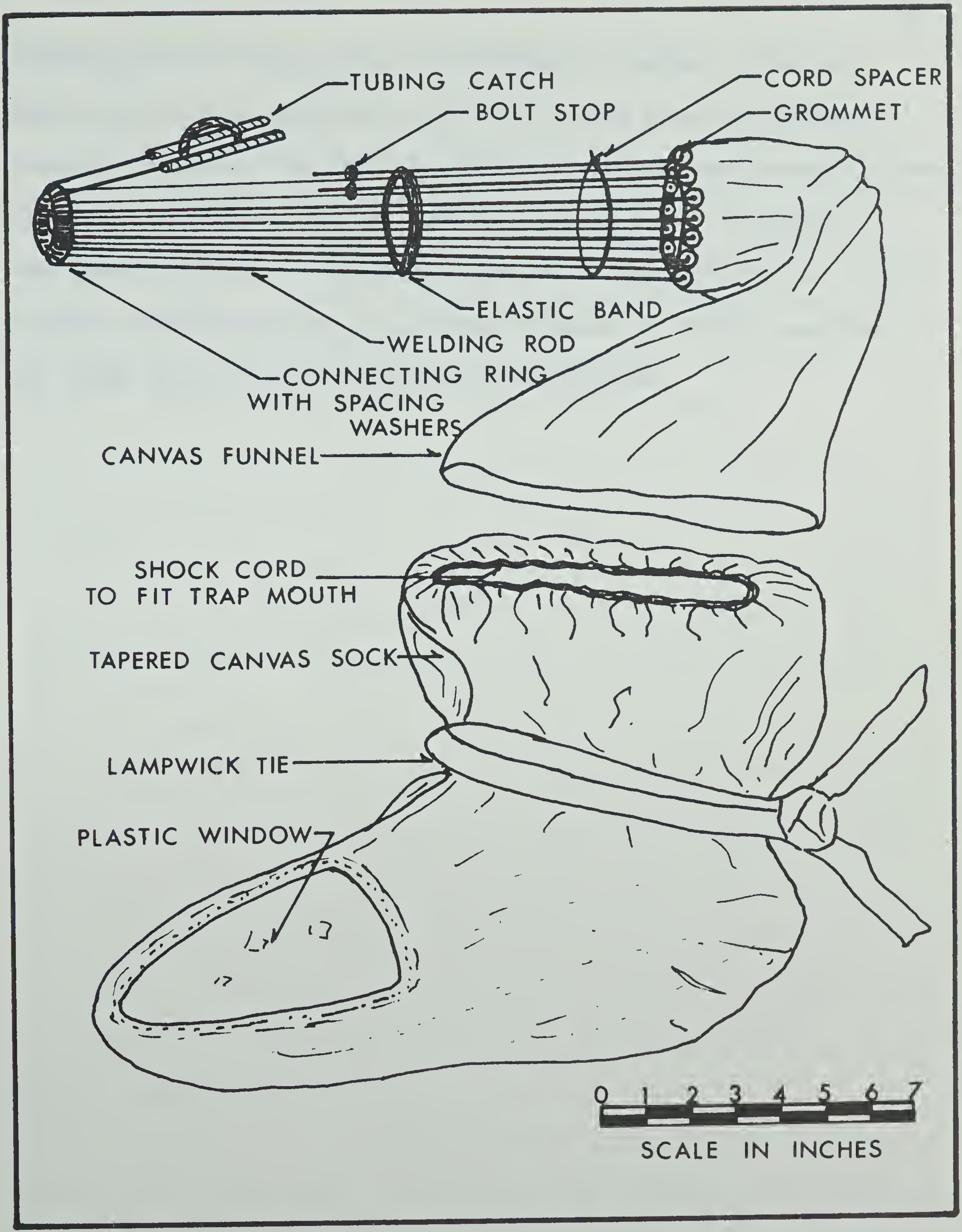


FIGURE 5 .WIRE HOLDING CONE AND CANVAS WEIGHING SOCK

extending from the home range to the point of capture. This was done subjectively, depending on opinions formed from the distance between the capture and the area where the squirrel was normally tracked, trapped and observed, and the proximity of the point of capture to the center of activity of another squirrel. This modification of the boundary strip method may be a closer estimate of actual range than the usual form of half the distance between traps.

AGING TECHNIQUES

Field differentiation of adult and juvenile animals was possible until the fall molt, with juvenile tail pelage noticeably thinner and body pelage resembling the winter adult in fineness, although not in density or color. Juvenile males could still be distinguished until initiation of reproductive development, there being a noticeably pigmented patch over the scrotal region in adult males and none in juveniles (Layne 1954). Non-parous females could be distinguished from parous in that nipples were present only as small pigmented dots until first lactation, and vulva size was much smaller. Closer examination revealed that although more criteria were available, they were not completely reliable: body size and weight differences were useful only until late summer.

Relative squirrel age was easily determined when an autopsy was performed. Reproductive tract condition was used to separate animals which had experienced a breeding season from those which had not. Regressed testes showed twisted venation, a thick, opaque tunica albuginea, and larger size than prepubertal testes. The latter had straight venation and a thin, translucent tunica (Layne 1954). Seminal vesicles, prostate and penis were also larger in adult males than in juveniles. In females the entire tract was larger in parous than in non-parous adults, and in the latter significantly larger than in prepubertal squirrels. Later evidence confirmed to my satisfaction that no sexually immature females were present in the breeding season, and none lived to the age of senility. Placental scars and corpora lutea were evident in fresh tracts of parous females to the initiation

of sexual development in the following year. Regression of the epiphyseal cartilage and closure of the distal suture of the femur could be used to identify animals less than 12 months of age without having to resort to X-ray techniques (Figure 6). An aging technique using degree of closure of the mid-sagittal crest suture was attempted, but was finally discarded as there was too much individual variation for accuracy in distinguishing between anything but extreme and already obvious age differences (Figure 6).

Although juvenile-adult age classes (subadult not used) were immediately evident and determined as the study progressed, the finer division of adult ages was only possible after all data had been collected. The method chosen was that of tooth wear classes. This was rather subjective and not wholly reliable, due to variations in rate of wear with differing food habits in different habitats, and due to the absence of known-age squirrels. However, evidence from live-trapping and size of final age groups suggested that the method was reliable enough for purposes of this study. Classes were: erupting, sharp cusps and sharp cusps showing signs of wear through year 1; rounded cusps and wearing through year 2; indistinct cusps and wearing so that enamel was visible only as traces between cusps through year 3; and gum line through year 4 (Figure 7).

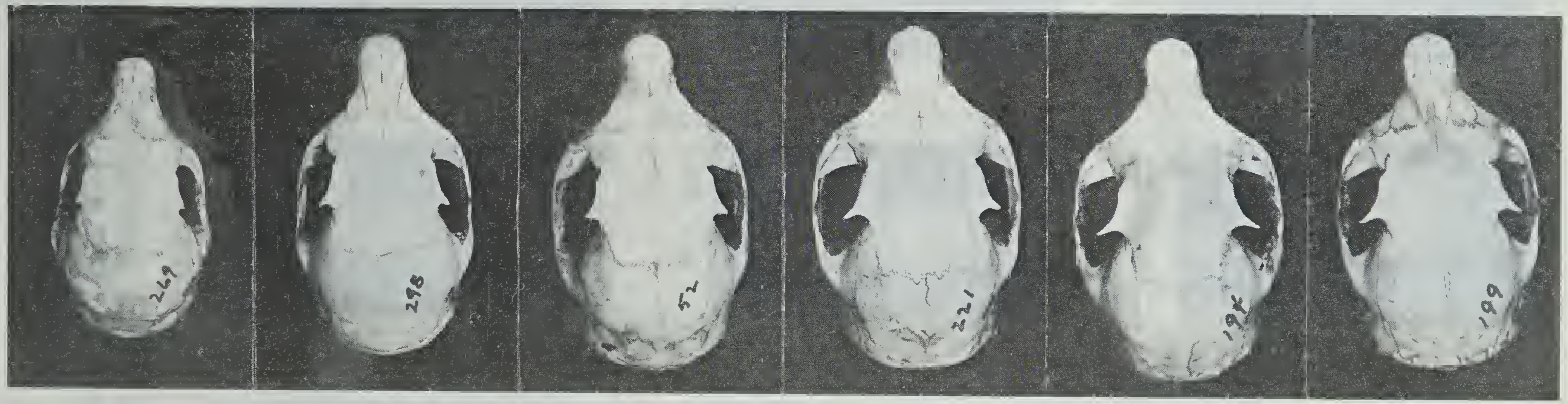


FIGURE 6 . APPEARANCE OF RED SQUIRREL SKULLS AND FEMURS COLLECTED AT VARIOUS INTERVALS AFTER THE MEAN BIRTHDATE.

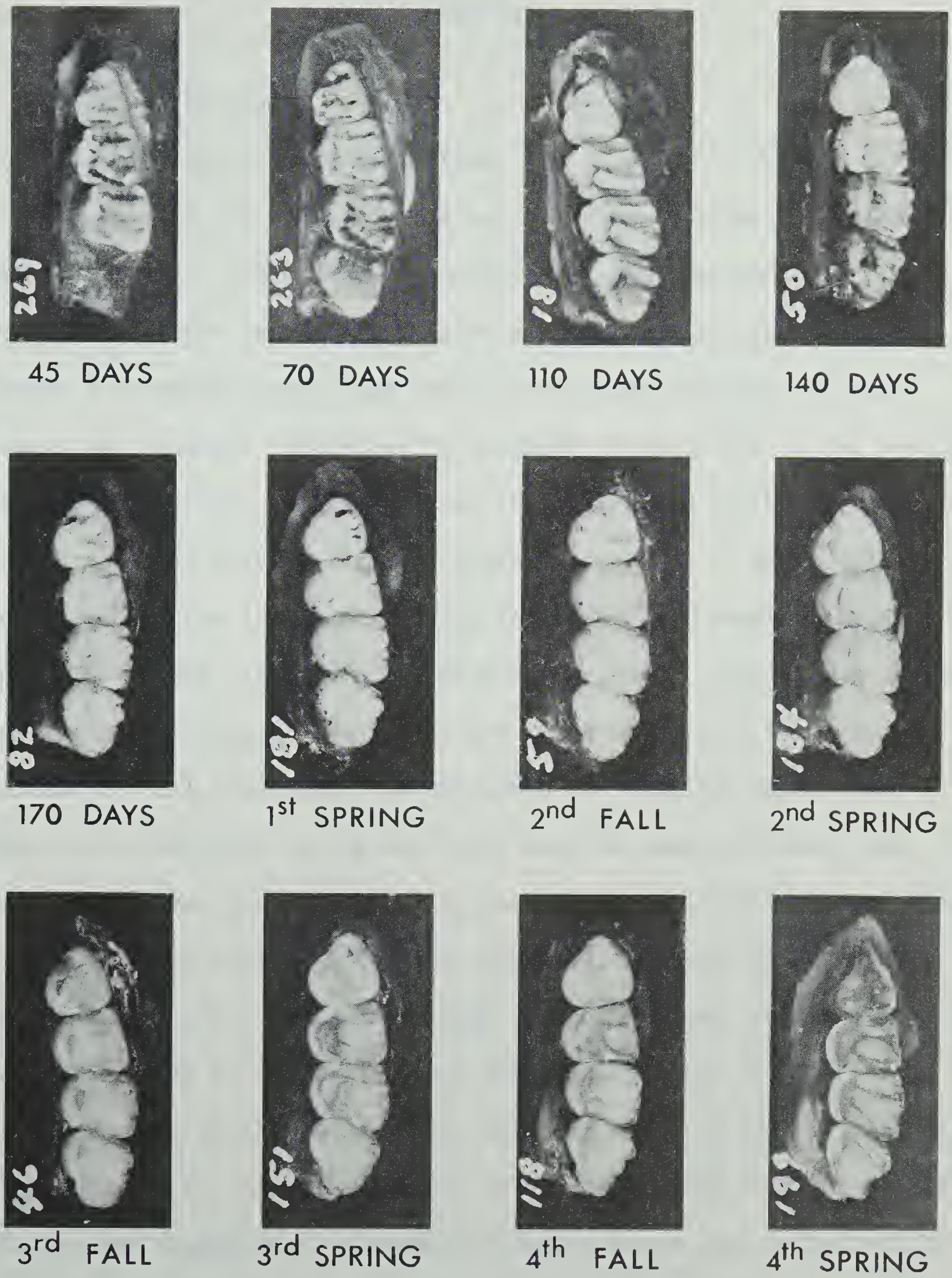


FIGURE 7. APPEARANCE OF UPPER CHEEK TEETH OF RED SQUIRRELS COLLECTED AT VARIOUS INTERVALS AFTER THE MEAN BIRTHDATE.

RESULTS

I. General Biology

i. Age classes and sex ratios

A sample of 300 red squirrels was taken for autopsy during the 14 months of study. Analyses were conducted to show age and sex composition of the population (Figure 8). Preliminary examination yielded a classical smooth age composition curve, steepest in the younger age classes. There was no evidence of squirrels living beyond their fourth spring, for by that age the molariform teeth were worn to the gum line and often broken. A seasonal division of age classes, separately for the 150 males and 150 females in the sample, yielded two different and irregular line graphs (Figure 8). The single litter recorded, consisting of one female and three male nestlings, was not included in this treatment, but reflected the slightly higher male to female ratio apparent during the first year of squirrel life. The ratio became less than unity in the second year and continued to decrease by increments occurring at regular intervals, to yield 100 per cent females by the final age group. This seemed to result mainly from gross reductions in the male cohort during the spring of each year. In each age class, spring peaks in the ratio of males to females preceded abrupt changes to ratios lower than in younger groups. It was assumed that the sex composition of seasonal samples accurately reflected the composition of the cohort which died naturally during the same period. Supporting evidence for the high spring mortality in males was found in activity data showing their extreme activity during breeding. This will be discussed in a later section.

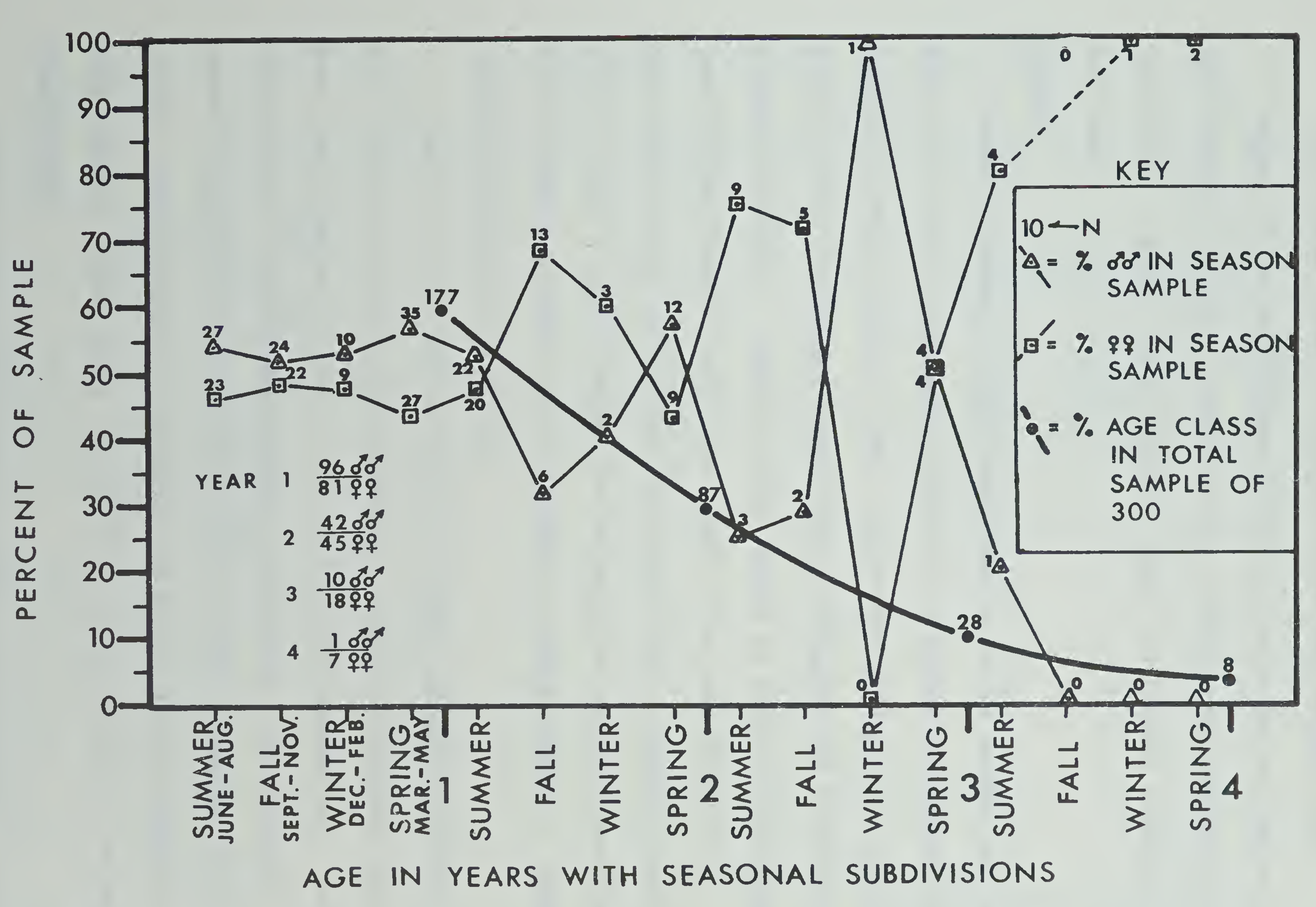


FIGURE 8 .AGE STRUCTURE OF THE RED SQUIRREL SAMPLE AND CHANGES IN SEX RATIO WITH AGE AND SEASON

ii. Gross seasonal changes in the reproductive tract

Organs of the reproductive tract in both male and female squirrels went through a distinct yearly cycle. This cyclic development and regression of gonads and accessory organs was treated separately for each sex.

Males:

Monthly changes in adult and juvenile testes weights are shown in Figure 9. Adult testes were smallest from August to October, with mean length 8.0 mm and width 4.4 mm. Testes were abdominal in position and flaccid, with a thickened bluish tunica albuginea and characteristic crenated venation. Juvenile testes showed no signs of development from June through November with mean length 4.8 mm and width 2.9 mm. These were rather solid, with a thin tunica and fine, straight venation. A slight weight increase marked the beginning of seasonal development in adults through November and in juveniles through December. Testes remained abdominal in position.

Testes of three adults taken in December showed increased weight, and in two of the three had descended through the inguinal canal. Mean length and width were 10.7 mm and 5.4 mm respectively. Data for adult males in January and February are lacking. In juveniles, the testes apparently did not show a sharp increase in weight until January, when descent of the testes and weight increase began to occur very rapidly. Mean length and width in January were 11.4 mm and 6.9 mm respectively.

Juvenile males in February had a mean testis length of 14.1 mm, width of 7.4 mm, and there was a recognizable scrotum by mid-month. Maturing sperm was recorded in 50 per cent of the samples, apparently

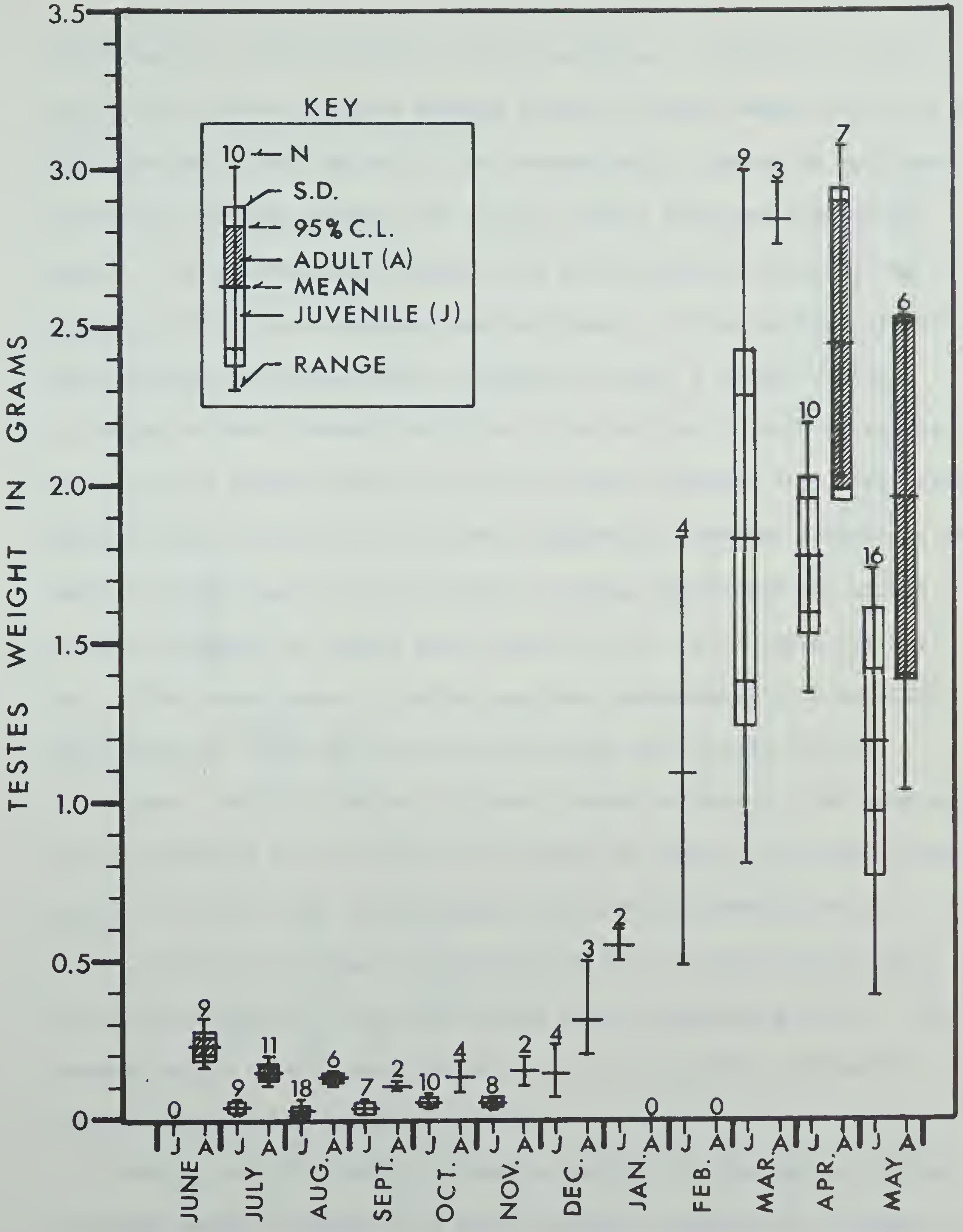


FIGURE 9. ANNUAL VARIATION IN TESTES WEIGHT FOR JUVENILE AND ADULT RED SQUIRRELS

initiated at a testes weight of about 1,000 mg. In March the testes in both age classes reached maximum size, with mean length and width of adult testes at 16.9 mm and 9.5 mm respectively. Testes of squirrels in both age classes became very turgid, with a thin and translucent tunica. The semeniferous tubules were much enlarged, about 0.5 mm in diameter. Veins were straight and enlarged. All testes were producing sperm through March and April, although in April a slight decrease in weight and measurements was noted. The scrotum through these months was large and pendant with a sparsely furred, darkened tip. Regression of the testes took place during May, apparently somewhat earlier in the month for yearlings than older males. During regression the testes rapidly softened, as though about one-third of the contents had been lost. The tunica began to shrink and turn opalescent, with venation again becoming crenated as the non-breeding adult condition was approached. Data for adults collected during May show 17 per cent with testes abdominal but all still with traces of sperm at the end of the month. In 44 per cent of yearlings, testes were abdominal and no trace of sperm was present by the month's end. Pooled data for May yearlings show 75 per cent with testes smears containing sperm. The scrotum became covered with longer fur as it atrophied, tip hairs growing in pigmented brown or reddish.

Seminal vesicle length followed a pattern of fluctuation similar to testes weight although with size increase in spring more sudden, and summer decrease much more gradual (Figure 10). In juveniles taken during March, only 10 per cent of seminal vesicles contained sperm against 100 per cent in adults. Seminal vesicles of juveniles were correspondingly much smaller. In April, seminal vesicle length in

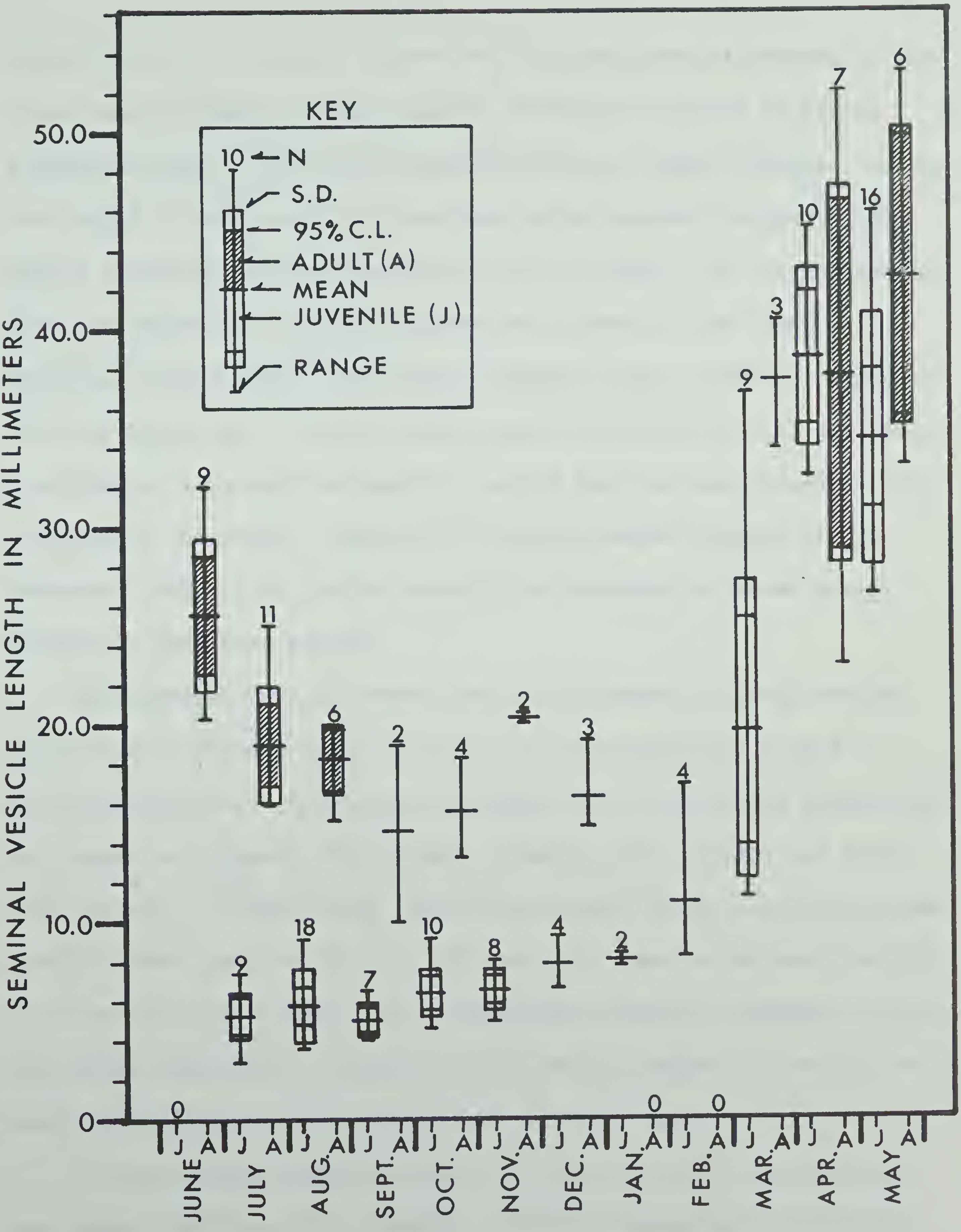


FIGURE 10. ANNUAL VARIATION IN SEMINAL VESICLE LENGTH FOR JUVENILE AND ADULT RED SQUIRRELS

juveniles was at its peak. There was no significant difference in the organ length between the age classes, although in adults it seemed somewhat thicker. All showed greatly enlarged, turgid tubules. In the last third of April and the first days of May several squirrels had partly empty seminal vesicles due to recent coitus. In the May sample, with the beginning of sexual regression in males, 75 per cent of yearlings showed seminal vesicles containing sperm, against 100 per cent of older squirrels. In that month seminal vesicles were all noticeably less turgid, although the length in adults had increased somewhat with collapse of the organ. During this period, seminal vesicle length decreased rather slowly with atrophy, but decrease in volume was apparently much more sudden.

Epididymides were all smear-checked for sperm, although swollen fluid-filled tubules, easily visible to the unaided eye, proved as good an indication. In rising yearlings 25 per cent showed epididymides with sperm in February, 90 per cent in March, all in April and 81 per cent in May. In older males, sperm was present during the latter three months. There were no data for this age-sex class in February, but 80 to 90 per cent with sperm in the epididymides could be expected. Peak development apparently occurred in April as in younger squirrels. No sperm was present in any organs of the male sex tract in June.

Prostate gland lengths followed the same seasonal fluctuation as the seminal vesicles, with juvenile and adult measurements remaining significantly different until the peak in April (Figure 11). Width of this organ averaged one millimeter less than length. No gross changes in appearance other than size were recorded through the year.

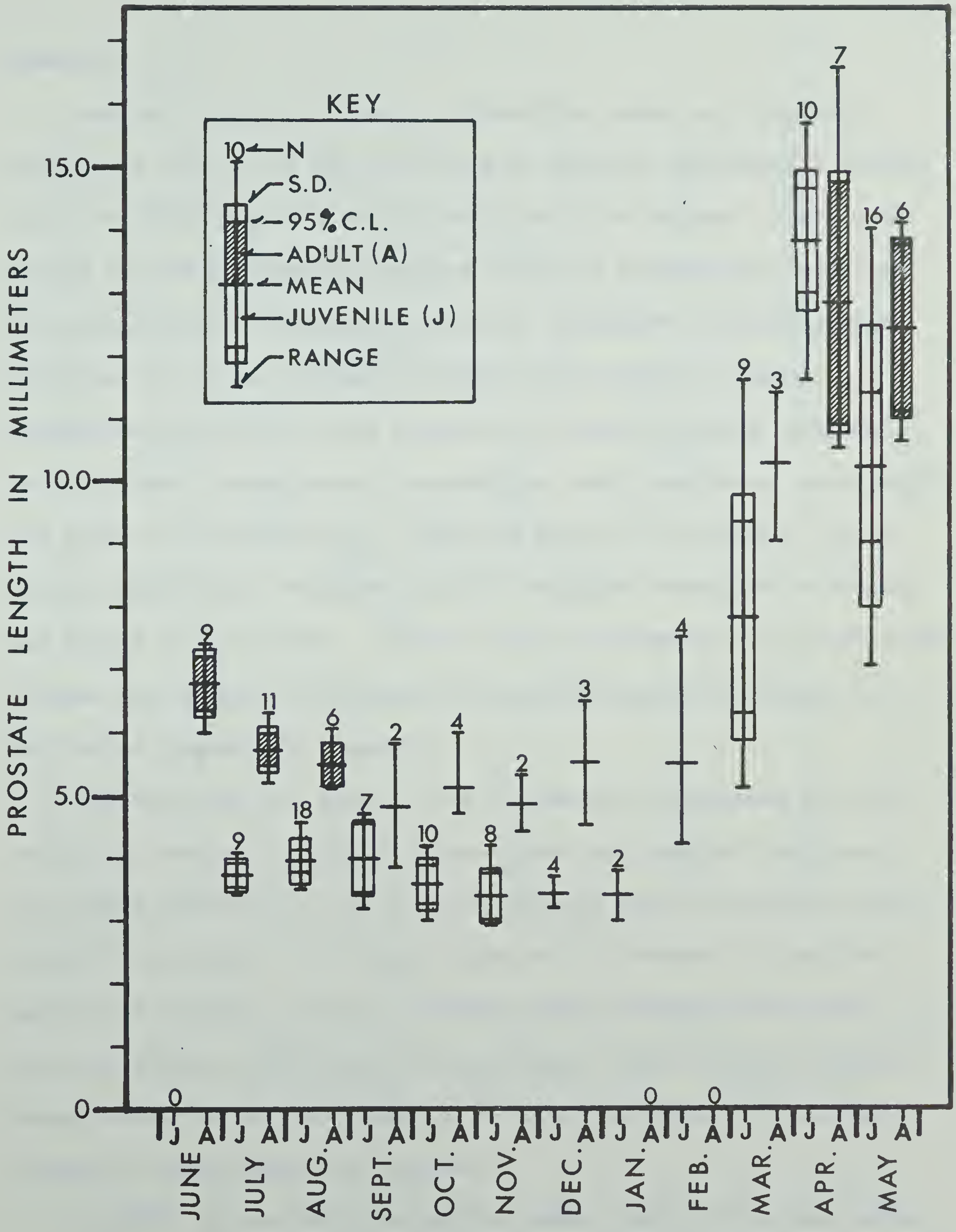


FIGURE 11. ANNUAL VARIATION IN PROSTATE LENGTH FOR JUVENILE AND ADULT RED SQUIRRELS

Females:

Seasonal changes in female reproductive tracts were much more pronounced than in the male, and several distinct reproductive classes could be recognized by size and condition of the organs. These were: parous anestrous (quiescent females which had successfully raised at least one litter), nulliparous anestrous (quiescent yearling females which had not become pregnant in their first breeding season), prepubertal anestrous, adult proestrous, puberty, estrous, pregnant, and lactating. Measurements recorded for each class were: mean length and width of uterine cornua, length and width of the ovaries, vagina diameter taken just below the junction with the cervix, vulva length, and length of the nipples. Uterine cornua measurements for these eight classes are recorded in Figure 12, ovary measurements in Figure 13, and vagina diameter in Figure 14.

Another class not shown in the figures was represented by only 4 of the 150 females collected. These three yearlings and one 2-year old became pregnant but did not give birth to young, resorbing their embryos before term. They were recognized by remnants of resorbing embryos or by early atrophy of mammary glands, mammae and corpora lutea associated with fresh placental scars. These criteria were no longer useful by mid-September, so any later specimens were probably classed as parous anestrous females.

In 1968, by back-calculating from summer data of that year using the 1969 sequence, parous anestrous females likely first occurred about July 1. The first change to proestrus with initiation of vaginal coiling was recorded on February 26 in 1969, and the last in parous anestrus on March 4. After the 1969 breeding season, the first

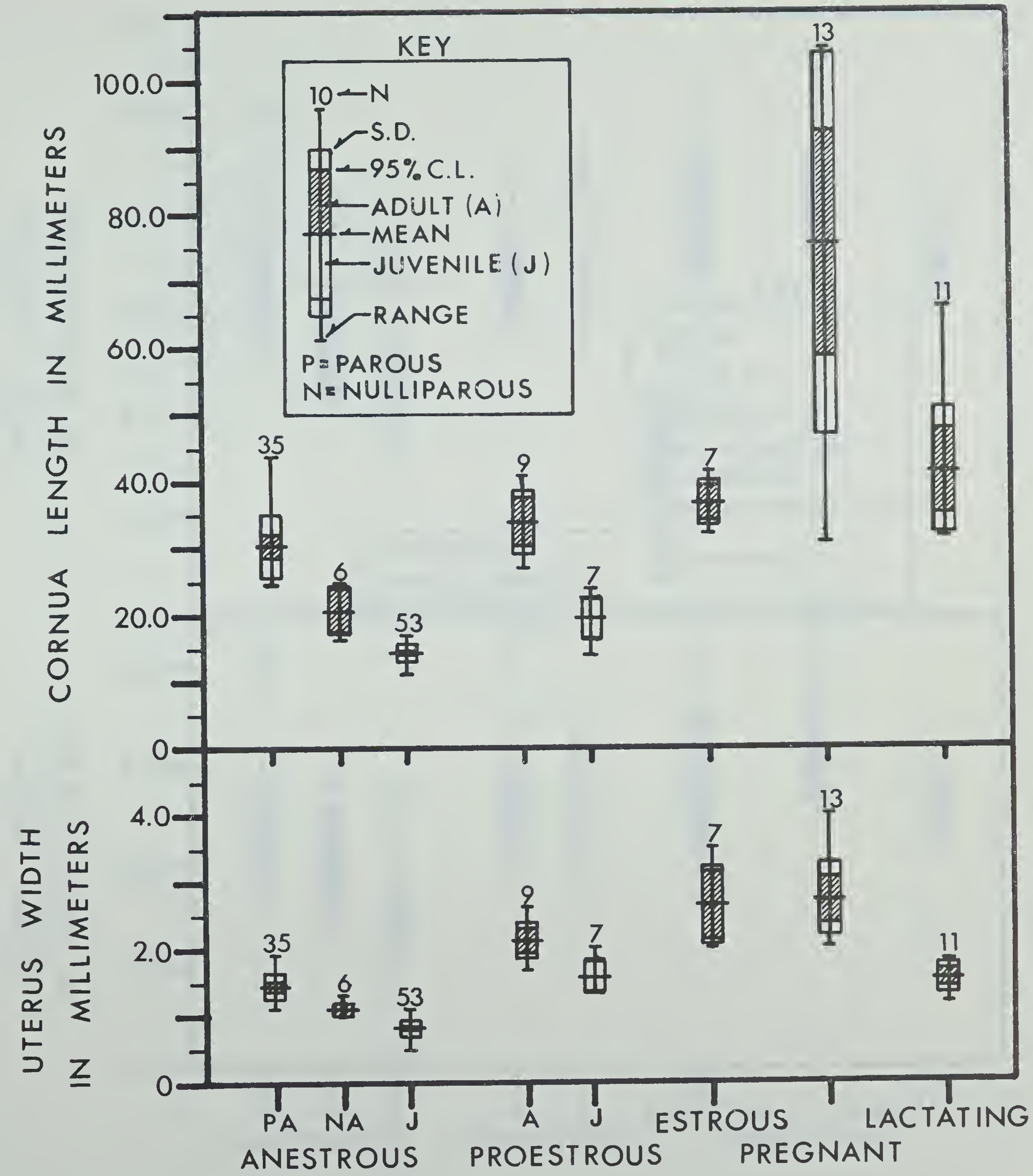


FIGURE 12. VARIATION IN UTERUS WIDTH AND CORNUA LENGTH CORRELATED WITH REPRODUCTIVE CONDITION OF RED SQUIRRELS

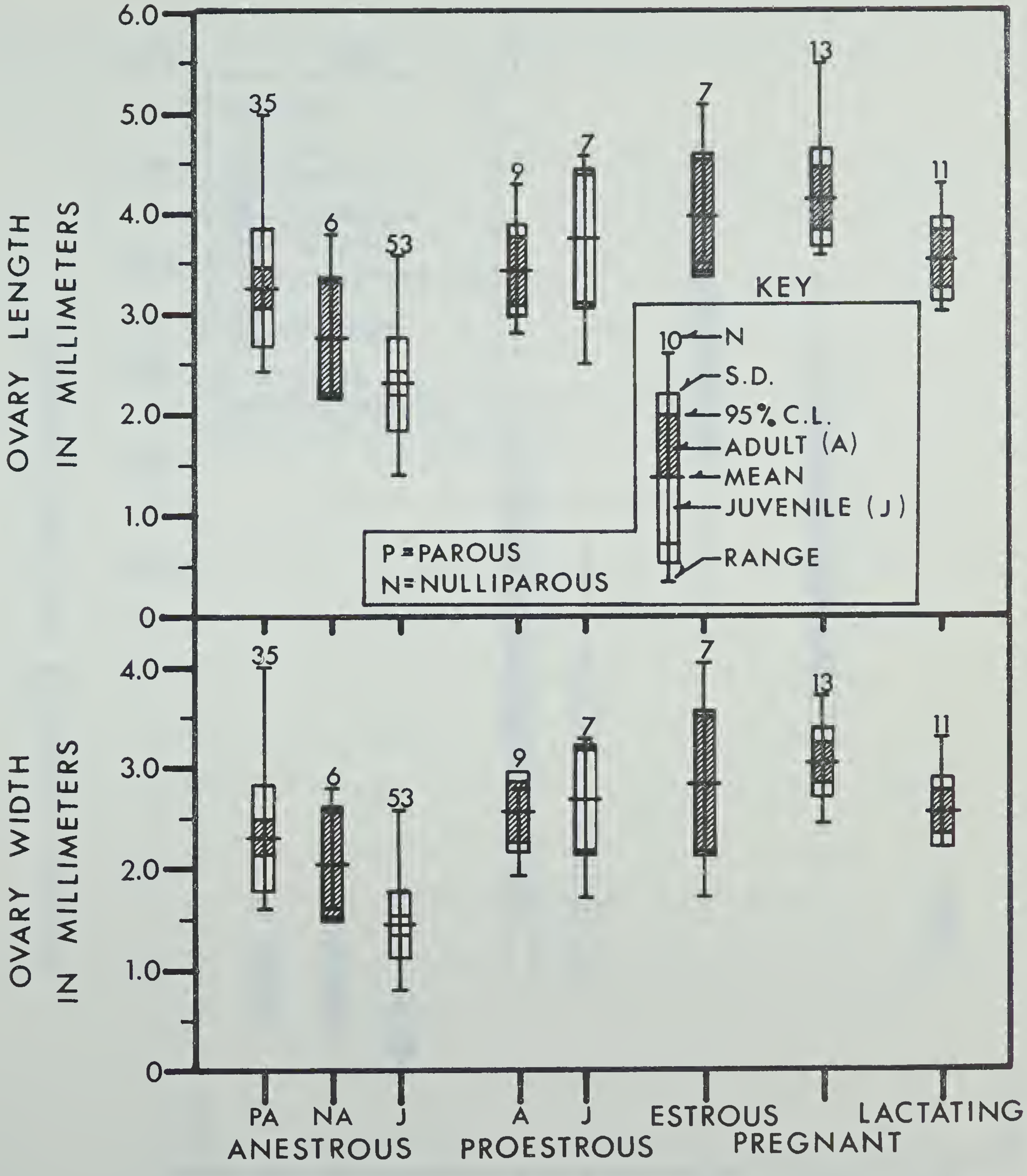


FIGURE 13. VARIATION IN OVARY LENGTH AND WIDTH CORRELATED WITH REPRODUCTIVE CONDITION OF RED SQUIRRELS

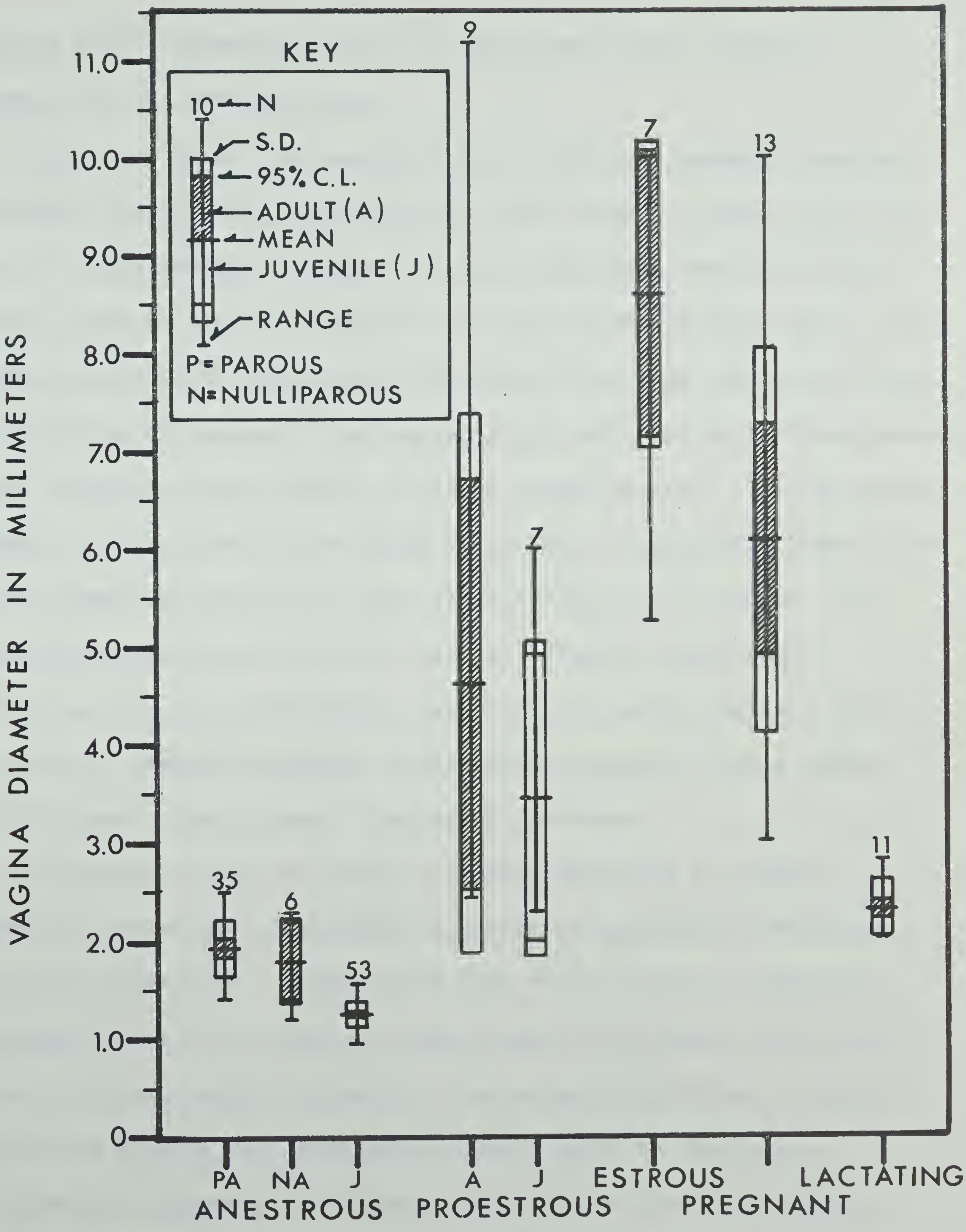


FIGURE 14. VARIATION IN VAGINA DIAMETER CORRELATED WITH REPRODUCTIVE CONDITION OF RED SQUIRRELS

anestrous adults appeared on July 25, three weeks later than was estimated for the previous year.

Fresh uteri taken from anestrous adult squirrels appeared somewhat translucent and flaccid, with placental scars clearly visible until the onset of the following proestrus. Corpora albicantia remained distinct as light brownish spots or bulges on the surface of the ovary until early December, after which they could still be seen for some time with the aid of a binocular microscope. The ovaries about that time became homogeneously opaque, resembling the juvenile condition except in size. The vagina was a simple, flaccid tube with no trace of coiling. Vulvae were imperforate for the caudal two-thirds and firm, about 4.0 ± 0.19 mm in length. The nipples after lactation were dark, heavily cornified projections 2.0 ± 0.18 mm long, and were hidden, especially in later anestrus, in the ventral fur. Nipples decreased in size during anestrus from a summer length of about 3 mm to about 1 mm before proestrus.

Reproductive organs of yearling females which had not become pregnant in spring were essentially juvenile in appearance, except for a slightly larger size. Ovaries were more visible than in juveniles, and showed traces of the spring activity until mid-October. The vulvae were as in parous adults but smaller, avaraging 3.2 ± 0.29 mm in length. Nipples were present only as minute brownish spots on the venter.

Juvenile (prepubertal anestrous) reproductive tracts were very small, with uteri opaque and solid. Ovaries were encapsulated in a bursa and usually difficult to find. There was no trace of vaginal coiling except in a few taken during their first post-natal month. Vulvae were typically anestrous in appearance, but somewhat smaller than in the previous two classes: 2.9 ± 0.14 mm in length. Nipples

were minute. This reproductive stage lasted from birth through to the beginning of proestrus about March 10, 1969.

Measurements of uterine cornua were highly significantly different between these three reproductive classes (P = 0.001). Measurements of ovaries and vagina were highly significantly different between parous and prepubertal anestrous females (P = 0.001). Ovary length was not different (P = 0.1), width was significantly different (P = 0.02), and vagina diameter was highly significantly different (P = 0.01), between prepubertal and nulliparous adult anestrous conditions. These latter measurements were not significantly different between parous and nulliparous adult anestrous conditions (P = 0.1, 0.3 and 0.4 respectively).

Proestrus began with initiation of coiling of the vagina, accompanied by a size increase in the other reproductive organs. Adult females had all entered this stage by March 4, 1969. The uteri became opaque and firm, and ovaries became granular with the appearance of many developing follicles. The greatest change occurred in the vagina, as shown by the extreme increase in range of the diameter measurement (Figure 14). It became elongate, turgid and tightly coiled - many times larger than during anestrus. The vulva enlarged to about 5.2 mm, becoming turgid, slightly pendulant, and deeper pink in color. It remained imperforate until the second week of April - the beginning of estrus for the adults collected. The nipples began to enlarge, becoming thicker but with little increase in length from the yearly anestrous minimum. Proestrus did not begin in juveniles until around March 10, 1969. At this time, differences in appearance of reproductive organs between the two age classes became slight. Uterine cornua

measurements were still highly significantly different (P = 0.001) and the nipples much smaller, varying from 0.1 mm to 0.3 mm in length, but other measurements were not significantly different from those of proestrous adults (P = 0.4). In juveniles this stage persisted until the third week of April - estrus beginning a week later than in older females in the sample.

Estrus in squirrels approaching their first year of age apparently occurred between April 20 and May 5, while older females in this condition were taken between April 18 and 23, 1969. Internally, the uteri increased slightly in size, becoming fully turgid. The ovaries became irregular in shape, with mature Graafian follicles appearing as viscous bubbles on the surface. Corpora lutea began to appear in mid or late estrus as opaque bulges 0.5 to 0.7 mm in diameter. In newly formed corpora lutea there was often a dark brownish blood clot. The vagina remained tightly coiled throughout this period, and the lumen was completely filled with desquamated cells, appearing as a mass of viscous white material. Externally, the vulva was firm, pendulant and swollen, about 6 mm in length. It had become perforate and bright red. The nipples continued to enlarge, on adults averaging 1.5 mm and on yearlings 1.0 mm in length. They showed some pigmentation.

After copulation there was an immediate change in the vagina. It was still coiled and of the same diameter, but no longer turgid. It became soft and thin walled with a much enlarged lumen filled with semen. The opaque white appearance changed to a bloody brown translucence. This was apparently a brief stage lasting only through active mating, as only two yearling females shot during mating chases, on May 4 and 5, showed this condition. One of these showed three new corpora lutea

but no sign of implantation sites, and the other showed what appeared to be two very new implants about 1 mm in diameter in the uterine wall.

Pregnant yearlings were taken from May 3 to June 3 and older females from April 26 to May 21, 1969. They were apparently present for about 12 days longer, but toward the end of pregnancy females became increasingly nervous and could not be collected. During pregnancy the uteri greatly increased in length due to growing embryos, although width measured between the implantation sites showed little change. There was a noticeable change in appearance, with the uteri becoming rather soft and vascular. The ovaries were enlarged and very irregular in outline, with much of their volume taken up by corpora lutea. Ovaries still appeared quite granular, apparently due to atretic follicles. The vagina gradually lost its coiling, and by the end of pregnancy was a short, flaccid smooth-walled tube 3 to 5 mm wide. Externally, the vulva became flaccid, averaging 5.6 ± 0.29 mm long and without the bright red color of estrus. It remained perforate however, and, as in late estrus, seemed to be constantly wet with discharge. Smears were heavy with leucocytes, especially just after ovulation and through early pregnancy, but little or no material from sloughing of the vaginal walls was found after the end of estrus. The nipples became swollen and increased in length to 2.5 ± 0.18 mm. Mammary glands began development about mid-pregnancy and by the end of term appeared as two white straps in the sub-dermal fascia, about 20 mm wide by 1.5 mm thick running the length of the abdomen. These were initiated in the inguinal region and developed cephalad, developing around the mammae first and then linking in a continuous strap on each side.

Timing of lactation was also distinctly different for yearling and adult red squirrels. In the collected sample, parous yearlings were lactating from June 16 to July 24, and older females from June 2 to July 8, 1969. A trend for older females to precede yearling breeders in reproductive development by one or two weeks was evident throughout the breeding season.

The uterus during lactation was much smaller than during pregnancy, and only slightly larger than in parous anestrous females. Placental scars showed as conspicuous dark bands. The ovaries had become somewhat smaller, but corpora lutea remained conspicuous and apparently active through lactation. There was no evidence of developing follicles, with ovaries no longer granular in appearance. The vagina was a simple tube, shorter and much thinner than during pregnancy but still larger than in the anestrous condition. The vulva became rapidly imperforate and firm as it atrophied to the anestrous appearance (mean length 4.6 ± 0.22 mm). The six, seven or eight nipples were very swollen and elongate (5.4 ± 0.28 mm long). The hair surrounding each had been shed late in pregnancy. The mammary glands appeared as two long white straps, becoming brownish late in lactation. At maximum development they measured about 28 mm wide by 2.2 mm thick. At the end of lactation atrophy progressed caudad, and no trace was left by August 12, 1969. It appeared that in 1968 this stage was reached some time in the first week in July.

iii. Fecundity

Corpora lutea counts were considered to yield good estimates of ovulation rates, due to their large size and persistence for many weeks after parturition. A comparison of these with placental scar

counts yielded information on pre-implantation loss as well as on litter size. One case of a polyovular follicle or a twinned ovum, where placental scars apparently exceeded corpora lutea, was recorded. Data are treated separately for the 1968 and 1969 breeding seasons, and for yearling and older females (Figure 15). In the same figure P-values are given comparing placental scar counts for these divisions.

It appears that reproductive success in 1968 was higher than in 1969, with a reduction in litter size between the two seasons from 4.0 to 3.4 young per female. A significant drop in numbers of placental scars was recorded between 1968 and 1969 for adults (Figure 15). Yearling females did not show a similar change in either the numbers of placental scars or corpora lutea (P = 0.1), but pre-implantation losses increased from 1.7 per cent in 1968 to 15.2 per cent in 1969. In adults these losses increased from zero in 1968 to 4.3 per cent in 1969. The three yearlings from 1968 and the five from 1969 which ovulated but failed to become pregnant were not included in this analysis. (Of these, the two not included for measurement in Figures 12 to 14 were in declining estrus when taken during the 1969 breeding season.) Also omitted were the four females from 1969 season which resorbed all developing embryos.

There was strong evidence for lower productivity in yearling than in adult females. In 1968 there was a highly significant difference in both corpora lutea and placental scar counts between the age classes (Figure 15). In 1969 there was no similar difference, with even a slight increase in yearling over adult corpora lutea counts (P = 0.5), but a 3.5-fold difference in pre-implantation losses between the age classes again resulted in a much smaller litter size for yearlings.

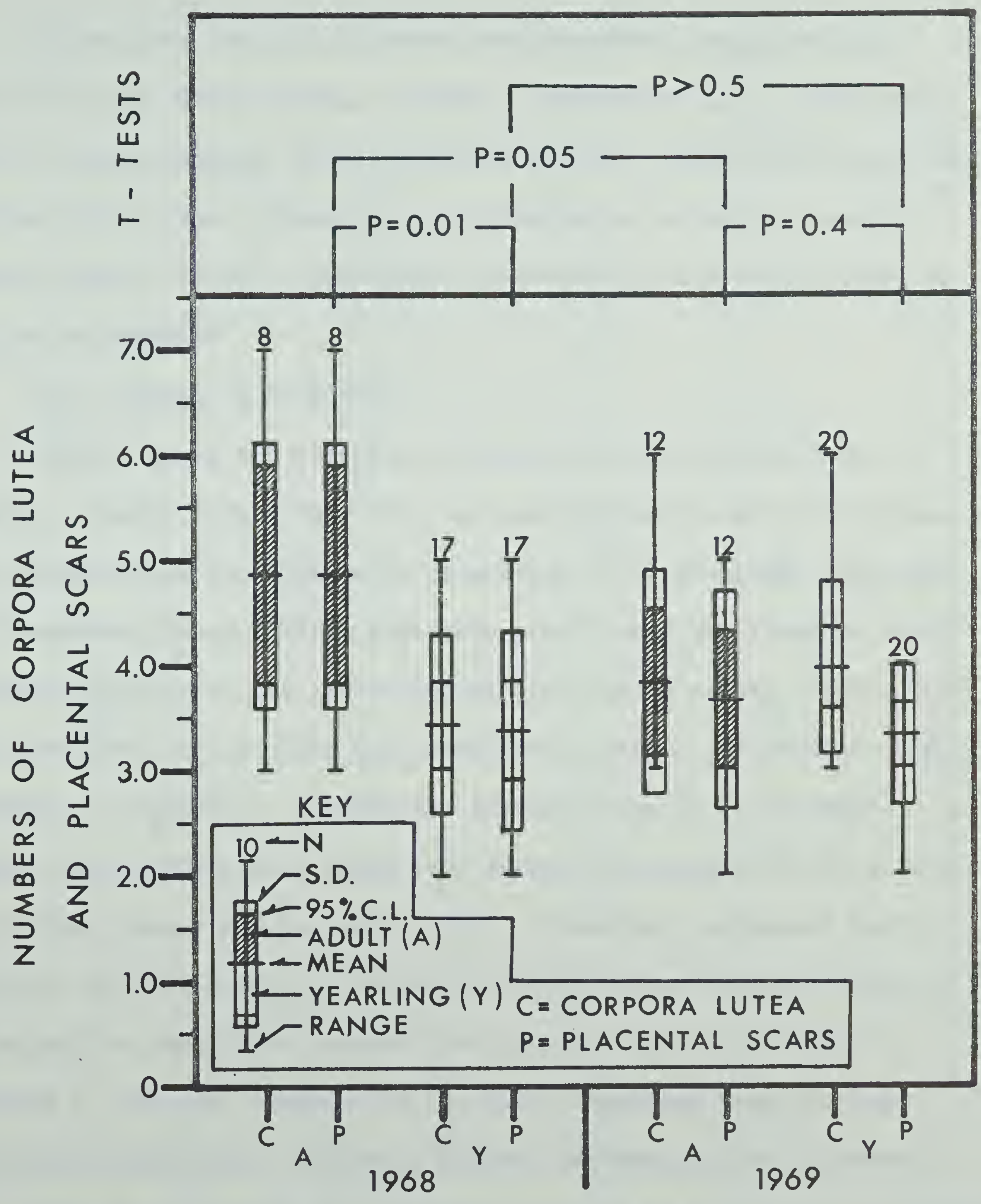


FIGURE 15. CORPORA LUTEA AND PLACENTAL SCARS AS INDICATORS OF PRODUCTIVITY IN YEARLING AND ADULT RED SQUIRRELS FOR 1968 AND 1969

All yearling females collected were apparently reproductively mature by their first spring, at about 10 months of age. Those which did not become pregnant still did enter estrus, ovulate and likely mate in their first year. There was no indication of a possible second, summer estrus. Further, there was no evidence of squirrels living to the age of senility.

iv. Growth of juveniles

A growth curve for juvenile red squirrels was derived from two sources of data (Figure 16). For the age interval from 45 to 92 days, body weights were recorded on 84 recaptures of 20 known-age weanlings and dispersing young. These squirrels constituted the juvenile cohort of the population on the live-trapping plot during summer, 1969. The data were used to calculate the predictive equation for growth: $\log Y = 1.787848 + 0.004938\,X$. For the age interval from 85 to 155 days, monthly mean weights were taken from juveniles autopsied in late July and through August and September, 1969. These data estimated body weight at approximately 90, 110 and 140 days of age, and were used to calculate the predictive equation for growth: $\log Y = 2.144751 + 0.001119\,X$. Further division of the data comprising these two age intervals produced four different slopes, decreasing with increased age: from 45 to 70 days, $b = 0.007281$; from 70 to 90 days, $b = 0.003505$; from 90 to 110 days, $b = 0.001672$; and from 110 to 140 days of age, $b = 0.000797$. As these results still describe a slight curve, even with all weights converted to logarithms, the juvenile growth rate was decreasing with age during this period at somewhat less than the exponential. However, correlation coefficients for the two straight line predictive equations given above were + 0.871399 (P = 0.001) and

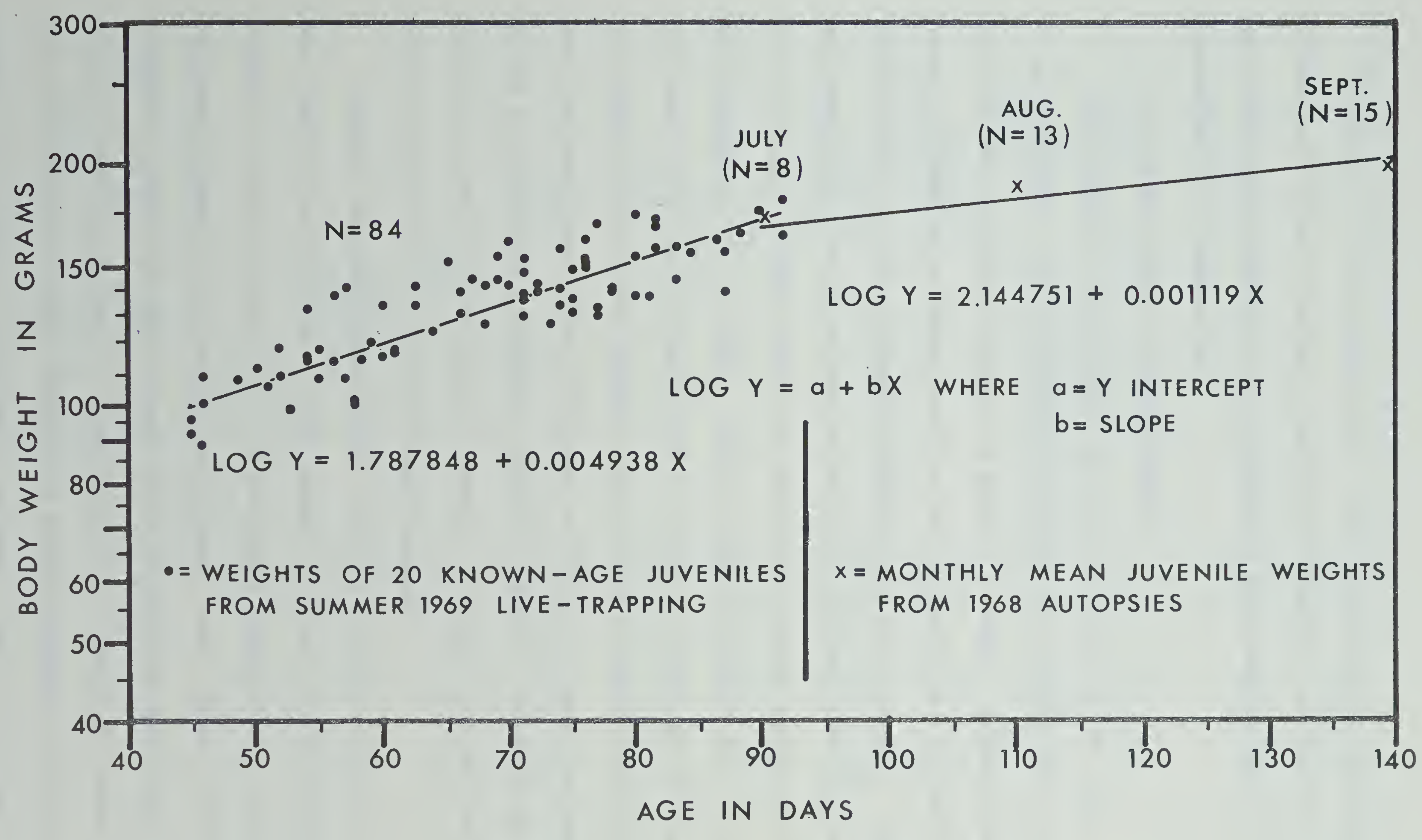


FIGURE 16 .GROWTH OF JUVENILE RED SQUIRRELS FROM WEANING THROUGH DISPERSAL

+ 0.977506 (P = 0.05) respectively. The equations were therefore proven statistically reliable, and may be used for calculation of age-weight relationships or for comparison with similar data on other subspecies of *T. hudsonicus*.

v. Body weights and measurements

Body weights at approximate age intervals during the first year of squirrel life, and at seasonal intervals for adults, were plotted for each sex to yield a picture of growth, seasonal variation and sexual differences as encountered in the autopsy data (Figure 17) (Body weights of the 13 pregnant females were not included). Growth was essentially over by an age of 140 days, although yearling weights still appeared somewhat less than the mean for adult males of 227.4$\pm$2.3 and females, 219.7$\pm$1.7 grams. Female weights averaged less than those for males except during the period of juvenile growth and during summer for adults. This latter exception was due to a weight gain in females from the usual mean around 215 grams to 226.1$\pm$2.9 grams, and was likely caused by the growth of mammary tissue in summer. There was no other significant weight variation with season, although both male and female adults apparently did show some slight changes.

Standard external measurements recorded as total, tail and hind foot lengths were plotted to show changes with age and differences between the sexes (Figure 18). It was again evident that the growth rate was highest in the younger age groups. Adult dimensions were reached at about 140 days of age, before which there was little of the sexual dimorphism evident in older squirrels. Growth in length of the hind foot appeared slight compared to growth recorded in total and tail lengths. The hind food apparently underwent most of its growth before

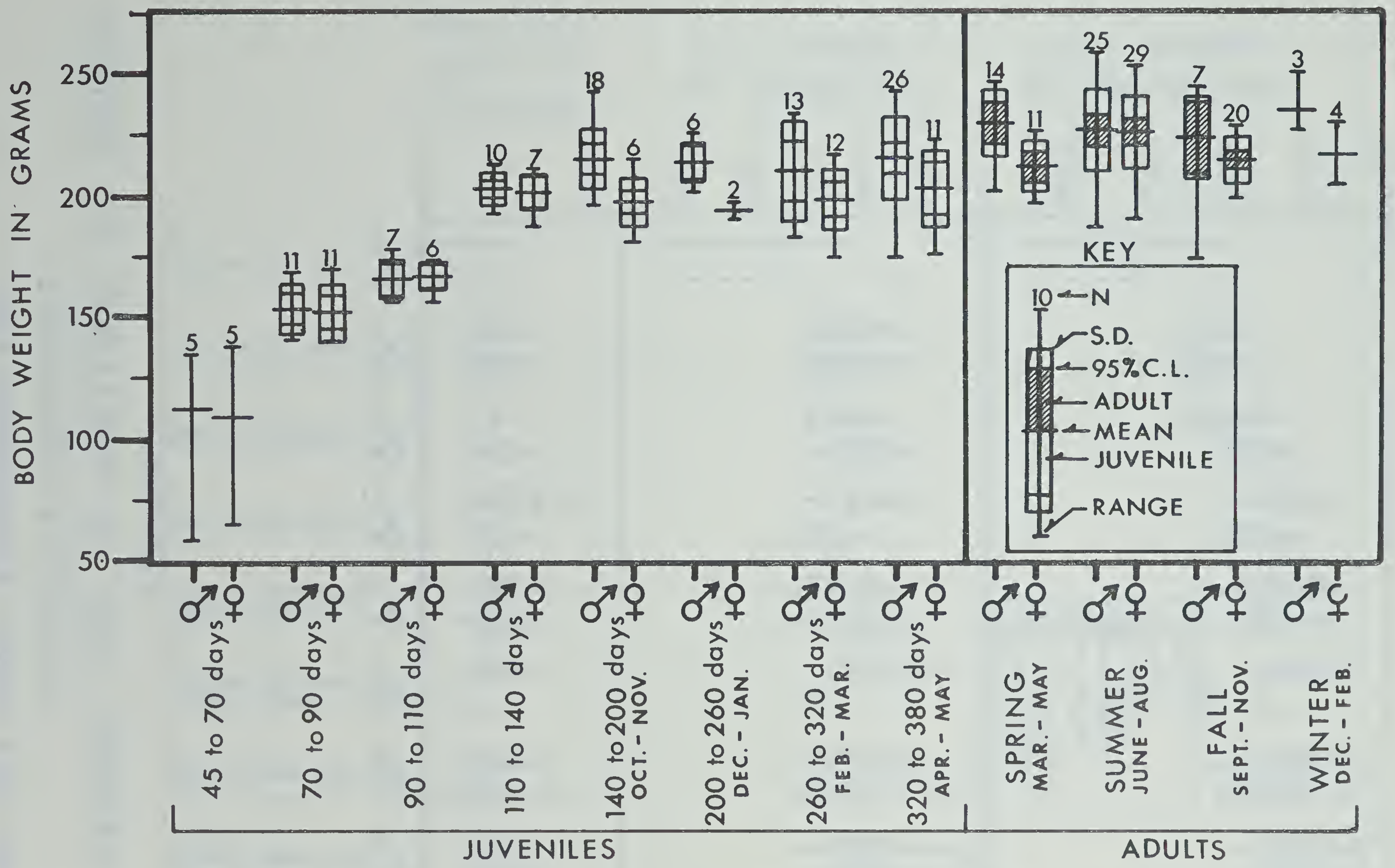
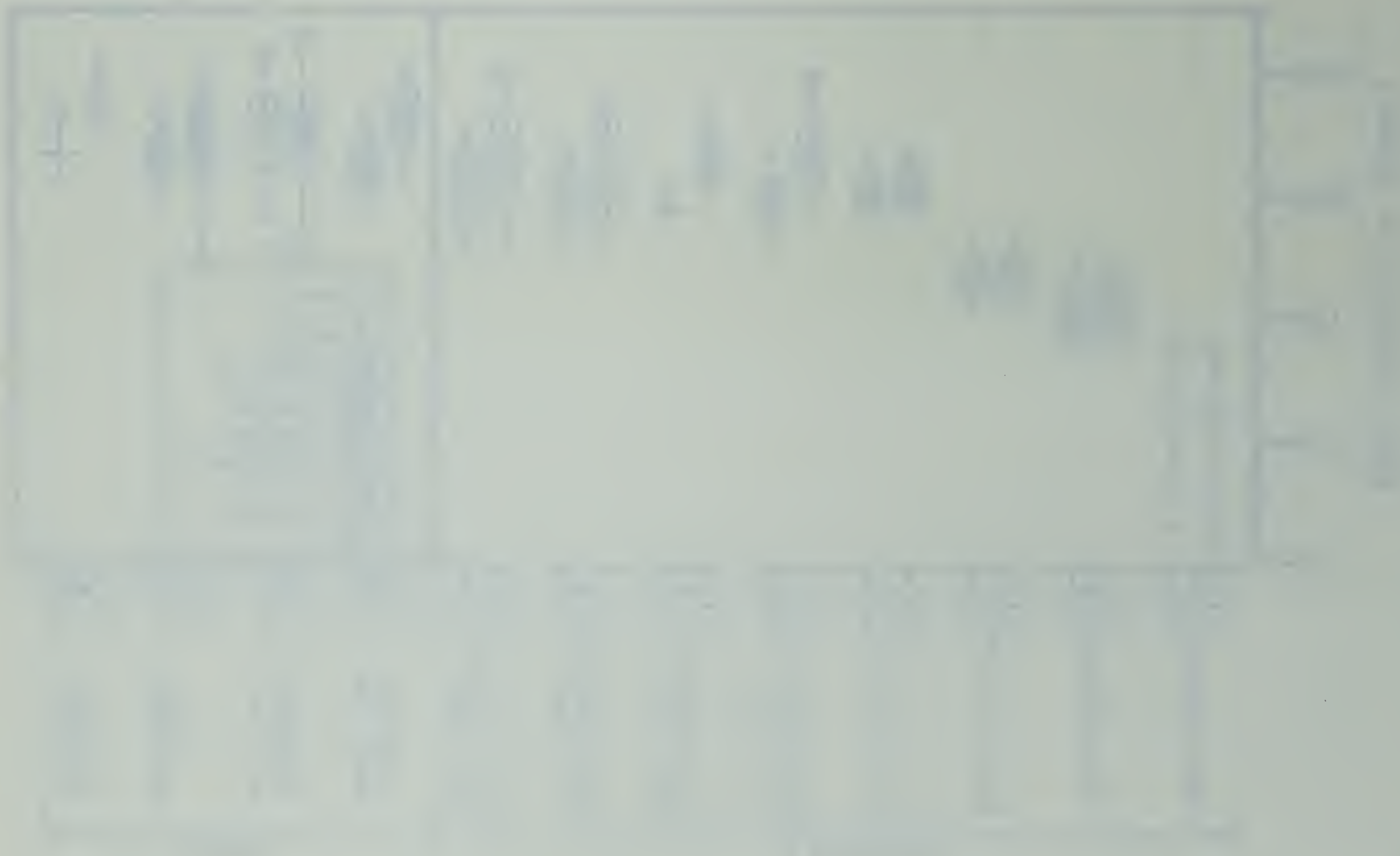


FIGURE 17 .VARIATION IN RED SQUIRREL BODY WEIGHT WITH AGE, SEX AND SEASON



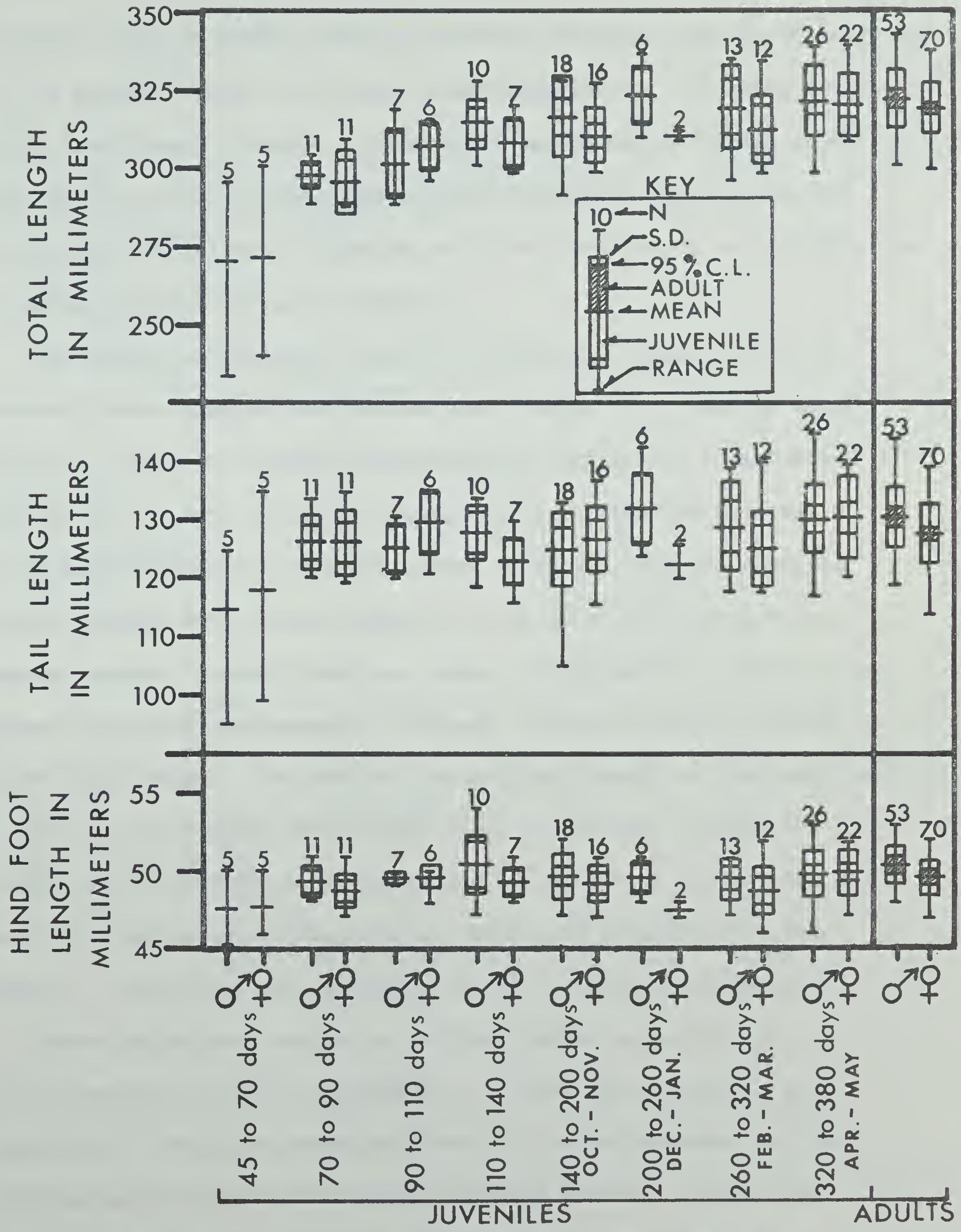


FIGURE 18 .VARIATION IN RED SQUIRREL STANDARD EXTERNAL MEASUREMENTS WITH AGE AND SEX

weanlings began to wander from the nest and therefore were first collected for the autopsy record. The final mean dimensions of juveniles did not differ from those of adults. Adult total length was 323.4$\pm$1.4 mm for males and 319.6$\pm$1.1 mm for females, body length was 192.4$\pm$0.9 mm for males and 191.2$\pm$0.7 mm for females, and hind foot length was 50.40$\pm$0.2 mm for males and 49.7$\pm$0.2 mm for females.

The length and breadth of skulls and length of mandibles were treated to show changes with age and sex (Figure 19). Results were similar to those for external measurements, with growth essentially complete by 140 days of age and males slightly exceeding females in mature measurements. During the period of growth, females appeared slightly larger than males, suggesting that females finish growing somewhat sooner. Growth rates and degree of variability seemed similar between the three measurements, although they may have been greater in the skull length. For adults, the greatest length of the skull was 47.98$\pm$0.14 mm for males and 47.60$\pm$0.09 mm for females, zygomatic breadth was 28.35$\pm$0.08 mm for males and 28.11$\pm$0.08 mm for females and mandible length was 33.03$\pm$0.11 mm for males and 32.85$\pm$0.07 mm for females. Variability was slightly greater in males than females.

Femur length was treated in the same manner as above, and similar remarks may apply (Figure 20). Growth was apparently more rapid than in skull and mandible dimension, as the increase in size from weaning to maturity was relatively much greater. Length and variability were again greater in adult males than in females, 41.36$\pm$0.12 mm and 40.50$\pm$0.09 mm respectively.

The upper cheek tooth rows reached adult length, 8.09$\pm$0.02 mm for males and 8.11 $\pm$0.02 mm for females, by about 60 days of age. By this

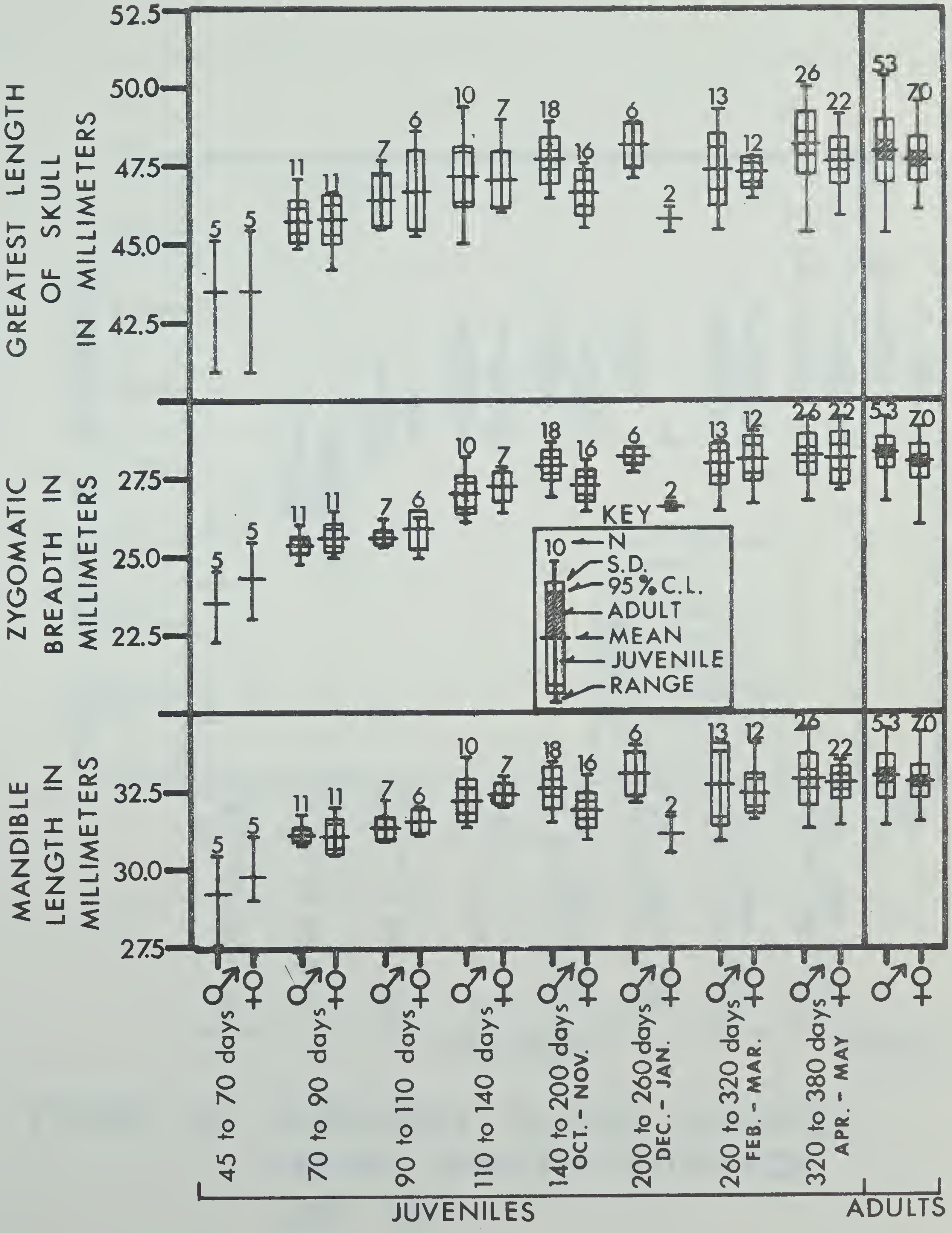


FIGURE 19 .VARIATION IN RED SQUIRREL SKULL AND MANDIBLE MEASUREMENTS WITH AGE AND SEX

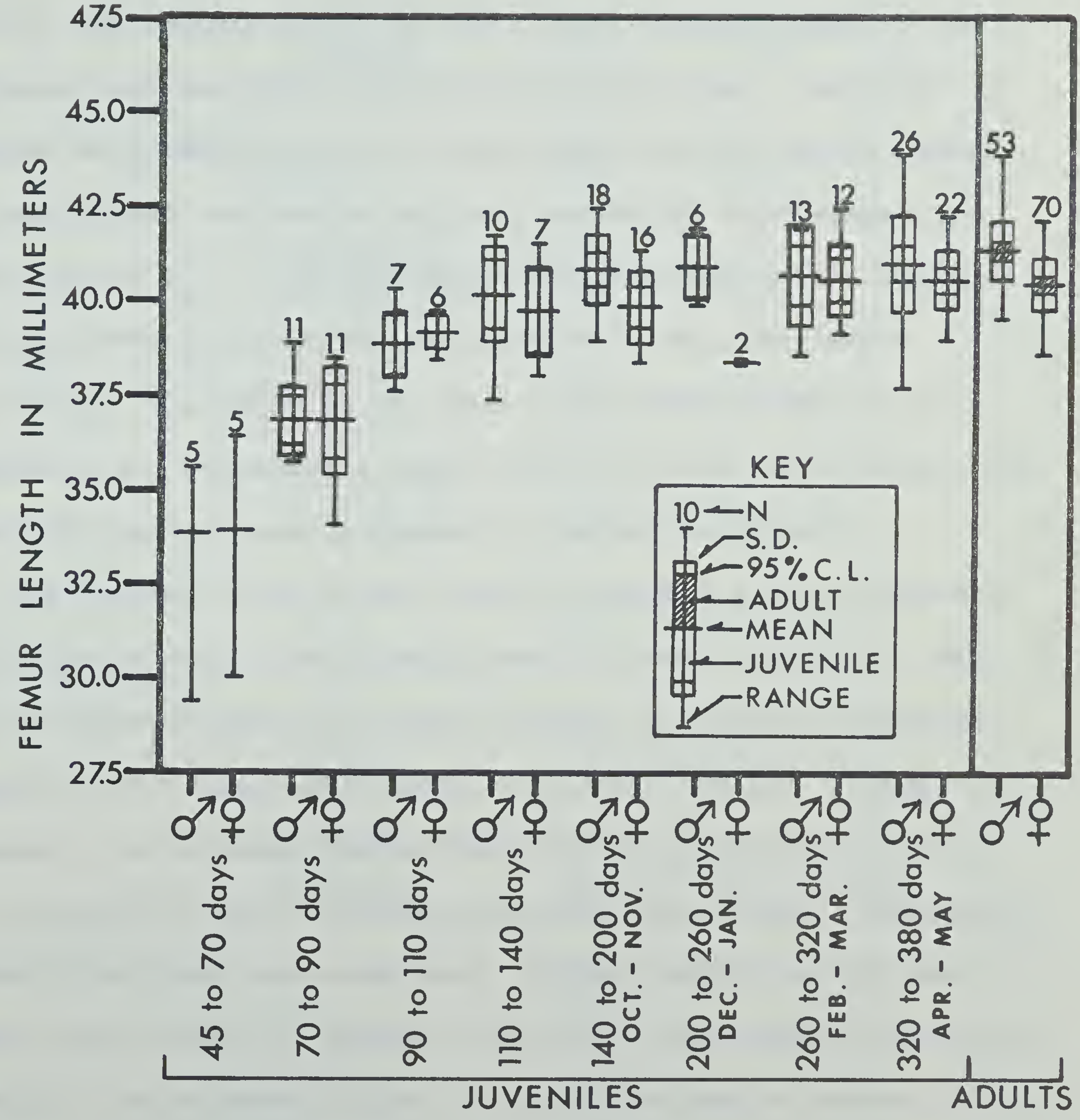


FIGURE 20 .VARIATION IN RED SQUIRREL FEMUR LENGTH WITH AGE AND SEX

age M_3 had fully erupted, and dentition on the maxilla consisted of three molars and one or two deciduous premolars. The permanent P_4 could be seen beneath dP_4 by 80 days of age, and had pushed out the deciduous tooth and fully erupted by 140 days of age. The third premolar was present in only 28.3 per cent of the 300 skulls examined, and when present was visible only as a minute peg close against the mesial root of P_4. It did not protrude to the level of the crowns of the other teeth and hence was not included in the crown length measurement. The length of the upper cheek tooth row was the least variable of all measurements taken, and the only one in which size and variability were apparently greater in females than males.

The combined weight of left and right adrenal glands relative to body weight of red squirrels was treated to reveal changes with age, sex and season (Figure 21). Adrenal weights of juveniles (examined seasonally) were larger than those of the adult groups. Although adrenals of males seemed heavier than those of females to 90 days of age, an opposite trend was observed in older age classes. Seasonally, however, there were some exceptions. Adrenal weights in fall were almost equal between the sexes, and in adults taken during spring the adrenals of males seemed slightly heavier than those of females. In rising yearlings, the adrenals of females were heavier than those of males, and in both sexes were heavier than those of spring adults. There was a definite seasonal cycle present. In spring, adrenal weights for female adults were similar to those for both sexes of adults in fall, but lighter than those of male adults. During the summer months of care for and dispersal of the young, adrenal weights were at their peak, and considerably heavier for females than males.

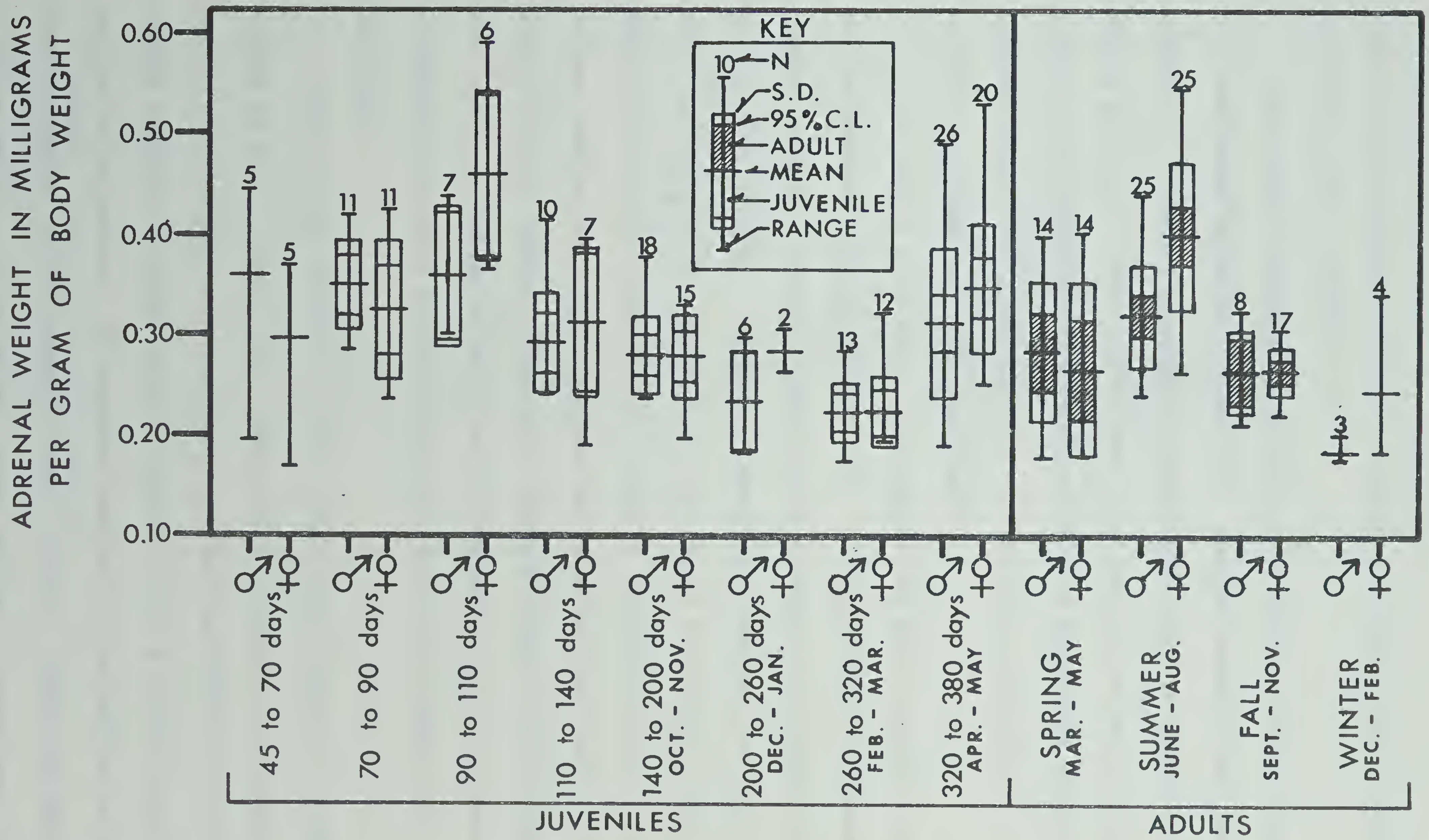


FIGURE 21. VARIATION IN RELATIVE WEIGHT OF RED SQUIRREL ADRENALS WITH AGE, SEX AND SEASON

Adrenals were smallest, and again larger in females than in males, during the winter months.

Red squirrel kidney weight relative to body weight was treated in the same manner as above (Figure 22). Results showed higher kidney weights in juveniles at weaning, and slightly higher weights during spring and fall. These latter were more distinct in the adult age class. Sex differences in kidney weight were apparently confined to the spring months, especially in adults, when considerably heavier kidneys were found in males than females.

Liver weight relative to body weight was also treated to show age, sex and seasonal changes (Figure 23). No significant differences were present with age, although there may have been a slight weight loss in the liver at weaning. Although highest liver weights for adult males were present in winter, this was likely an artifact due to small sample size, as the remainder of the data suggest a slight cycle of highest weights in summer when food was abundant and lowest with energy drain in winter. Male liver weights seemed slightly higher than those of females at all ages after physical maturity, except for a temporary reversal in adults during summer when females were lactating.

Spleen weight relative to body weight was treated in the same manner as above (Figure 24). There was no evidence of a change with age. In physically mature squirrels a trend was observed for male spleen weights to exceed those of females, with a possible exception in adults during winter. The argument against this exception is one of sample size as in liver weights above. Finally, there may have been a slight yearly cycle of higher spleen weights in summer and lower

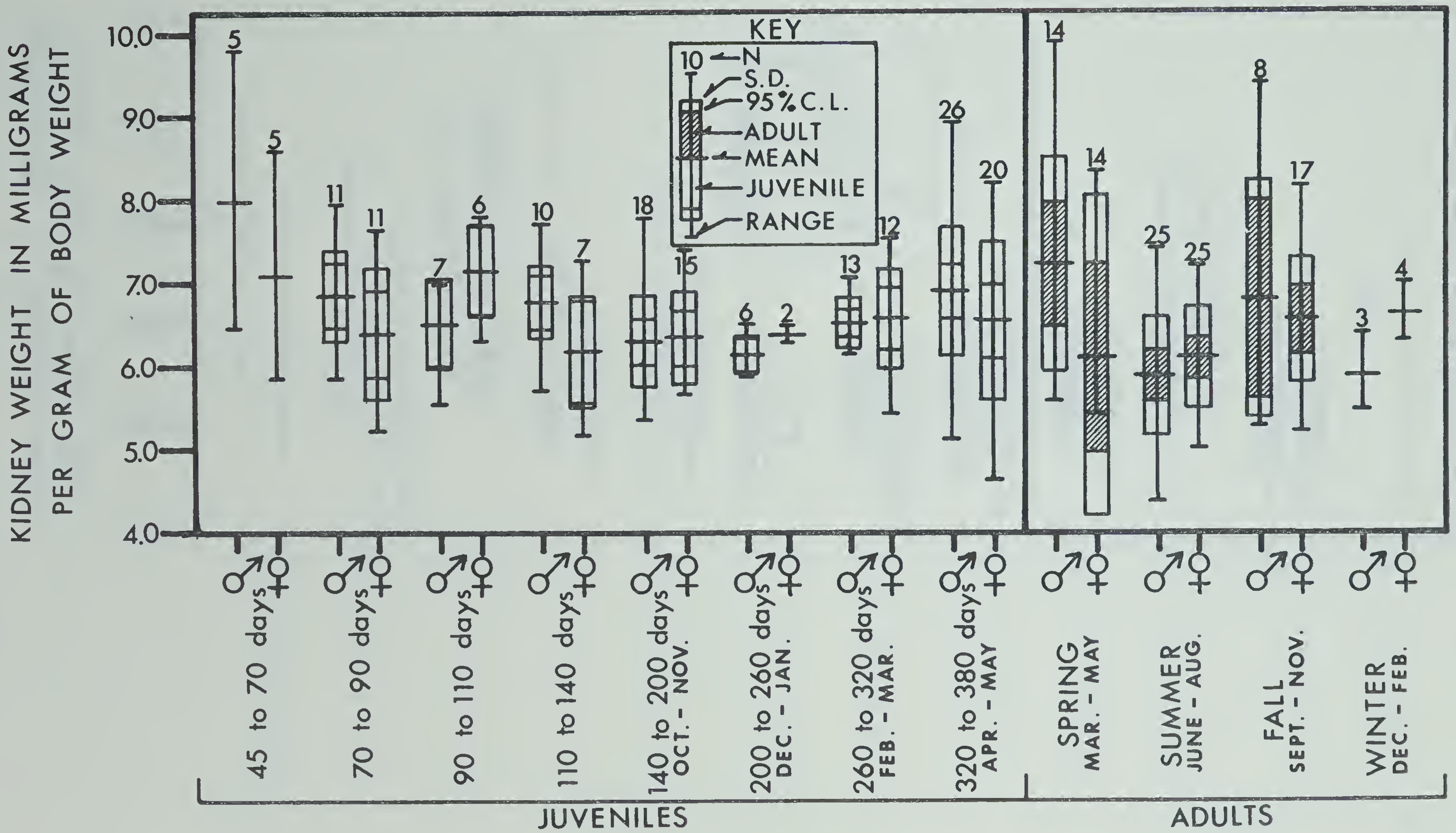


FIGURE 22. VARIATION IN RELATIVE WEIGHT OF RED SQUIRREL KIDNEYS WITH AGE, SEX AND SEASON

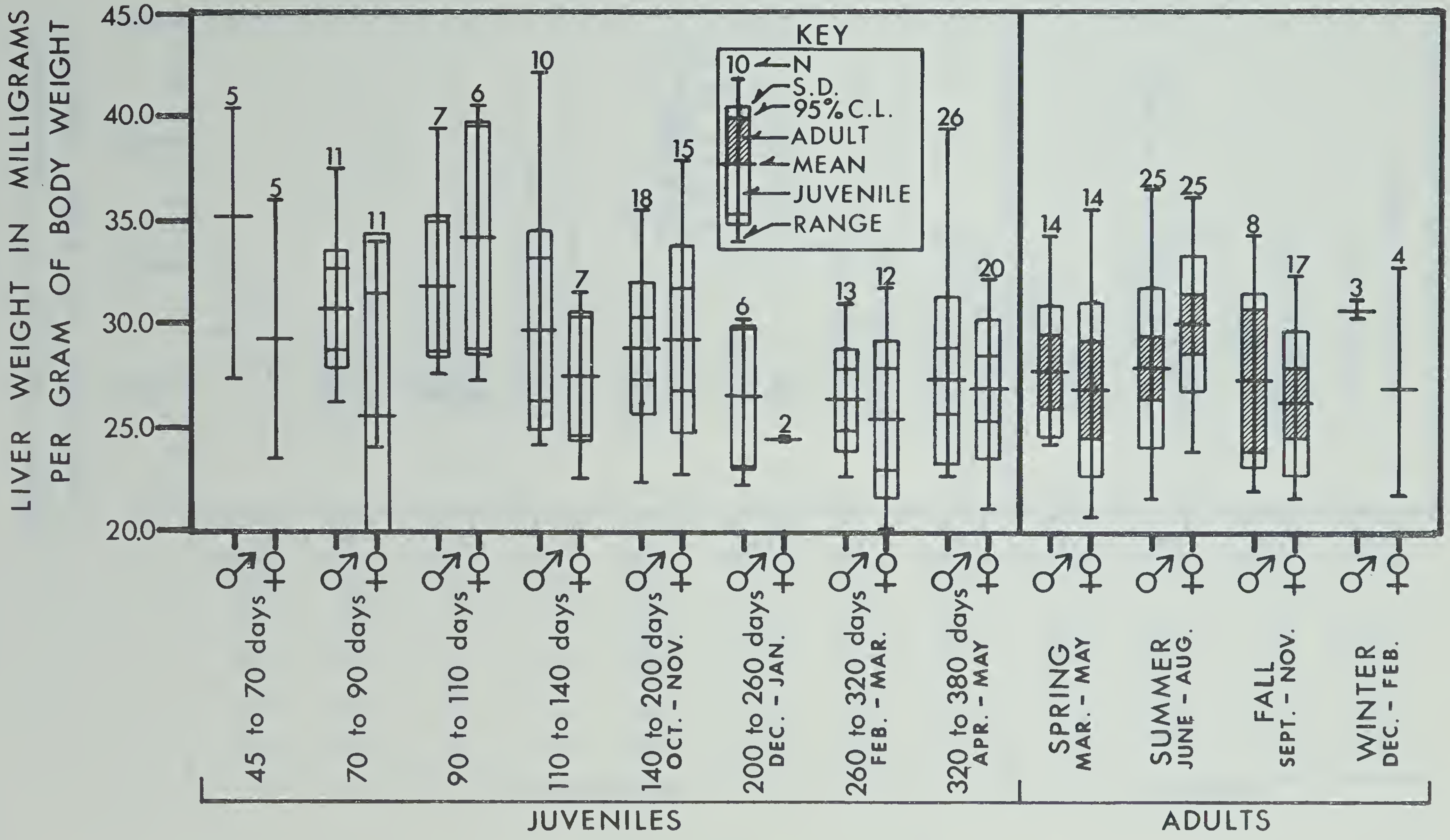


FIGURE 23 .VARIATION IN RELATIVE WEIGHT OF RED SQUIRREL LIVER WITH AGE, SEX AND SEASON

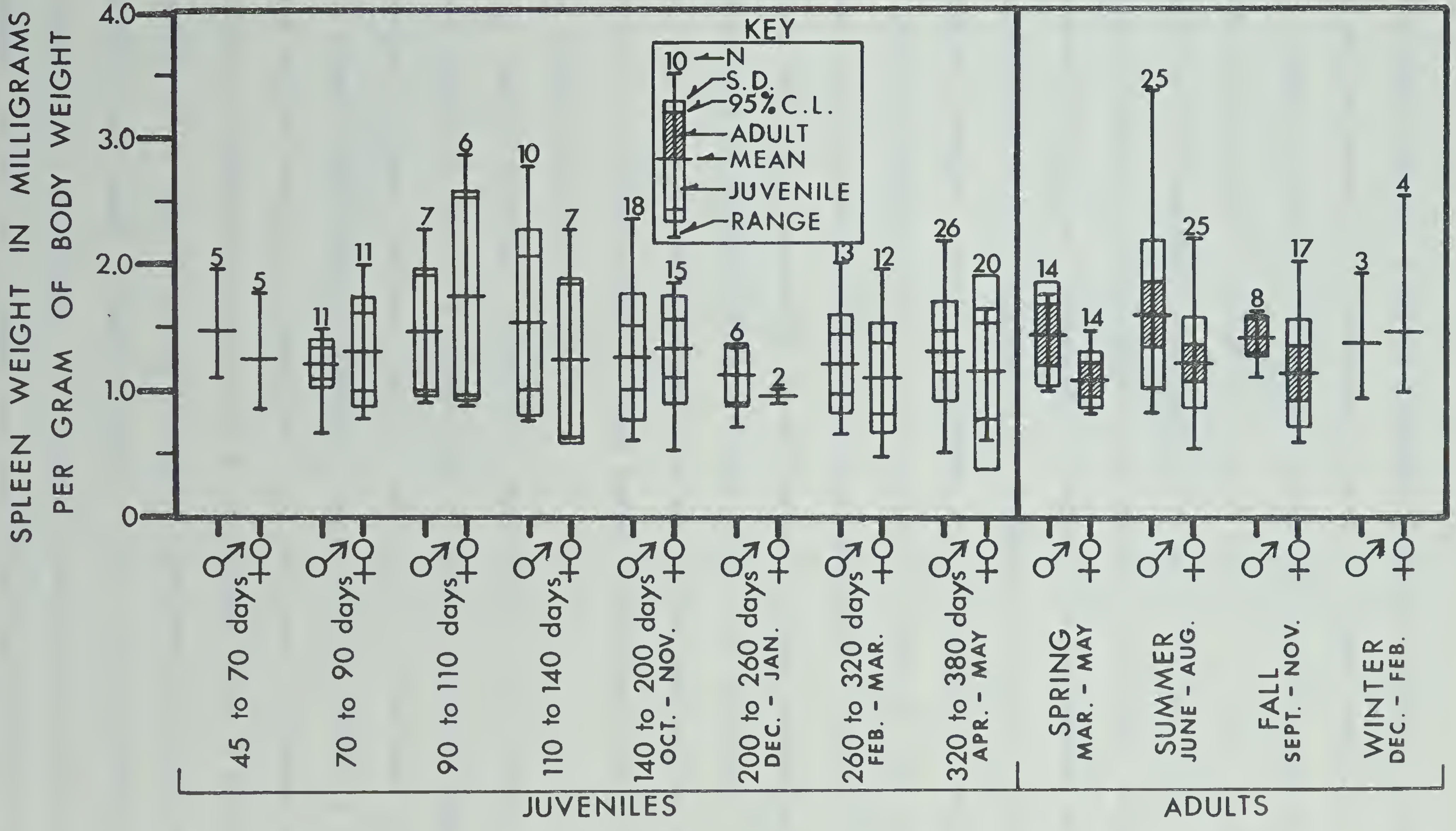


FIGURE 24 .VARIATION IN RELATIVE WEIGHT OF RED SQUIRREL SPLEEN WITH AGE, SEX AND SEASON

in winter, although a winter increase almost to the level of summer values was possible, as previously noted, for adult females.

Brown fat deposits were found along the sciatic nerve, above the heart, between the scapulae and in each axilla, but only the axillary deposits were measurable throughout the year. Weights of one of these, relative to body weight, were treated to show age, sex and seasonal differences (Figure 25). Changes with age seemed confined to unseasonally high weights in the youngest age class recorded. Seasonal changes occurred on a marked cycle with heaviest weights in winter and lightest during the warm months. There was some suggestion that the brown fat cycle was of greater amplitude in females than males. Brown fat weights generally seemed heavier in males during spring and summer and in females during fall and winter. In yearlings, however, axillary brown fat deposits remained heavier in females than males through the spring as well. These sexual differences were too slight for statistical significance.

Anal gland weights relative to body weight were treated in the same manner as above and yielded nearly opposite results (Figure 26). Changes with age consisted only of rapid growth of the anal glands to the summer peak weights. Seasonal changes recorded showed a cycle with peak weights during the summer and fall and lowest in winter and spring. There was again some evidence for a greater amplitude of this cycle in females, with female anal gland weights considerably higher than in males during summer, slightly higher in fall, and considerably lower through winter and spring. The change in anal gland weight in adult females from spring to summer was significant, and reflects similar changes in activity and size of home ranges recorded in the following major section on live-trapping studies.

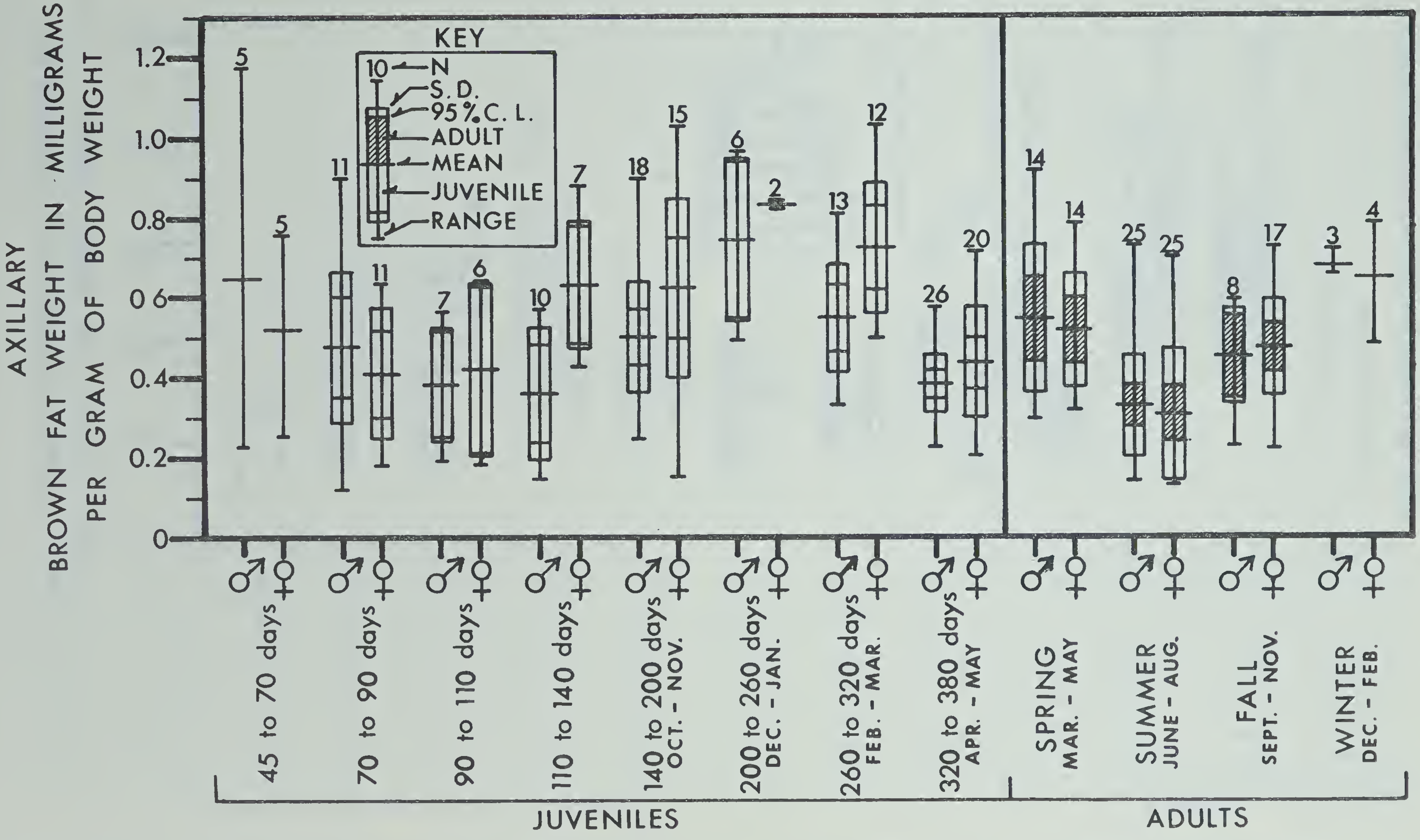


FIGURE 25 .VARIATION IN RELATIVE WEIGHT OF RED SQUIRREL AXILLARY BROWN FAT WITH AGE, SEX AND SEASON

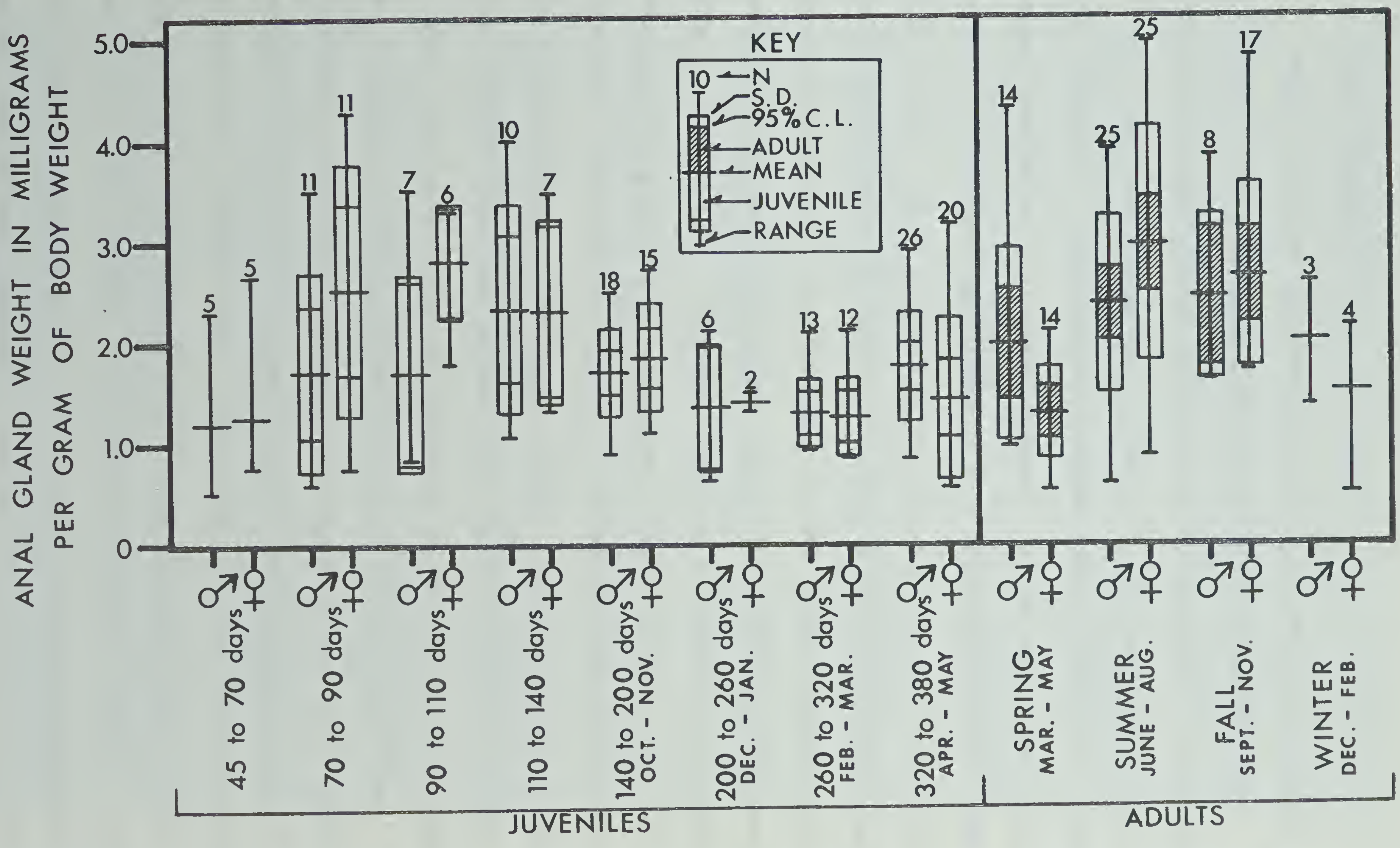


FIGURE 26 .VARIATION IN RELATIVE WEIGHT OF RED SQUIRREL ANAL GLANDS WITH AGE, SEX AND SEASON

vi. Pelage

Pelage condition and priming patterns of red squirrel pelts collected on the study area revealed two major molts each year. Representative pelts taken from this collection showed the spring molt to be a long process beginning in early or mid-February and lasting into June (Figure 27). The molt was observed first in males, the scrotum pelage changing as the testes descended. By the end of February, both sexes usually showed small areas of molt and new hair growth under the chin as well. Early progress of the molt was slow, and by the end of March included only the tip of the snout, a line between eyes and ears, the dorsal surface of the forefeet, and two patches running from the corners of the mouth down either side of the throat to cover the upper chest. Through April, a gradual expansion of these molting areas showed new hair growing on a inverted Y-shaped patch on the crown, and extending caudad from the ears along the sides of the neck to end in a few obscure patches on the upper abdomen. Before breaking up, this line included medial and lateral edges of the forelimbs, extended slightly into each axilla and completely covered the dorsal surface of the forearms. By early May and through to mid-month, molt was increasing, progressing caudad on the dorsum and moving proximally on the dorsal forelimbs. Other than the completed molt on the mid-line of the throat and upper chest, and in males over the perineum, there was no further hair regrowth on the venter at this time. In the last half of May, however, molt began to occur very rapidly. By the end of May it had progressed up the outside of the hind limbs and caudad down the back, apparently passing onto the venter and inside the limbs as it progressed. By mid-June the spring molt was complete

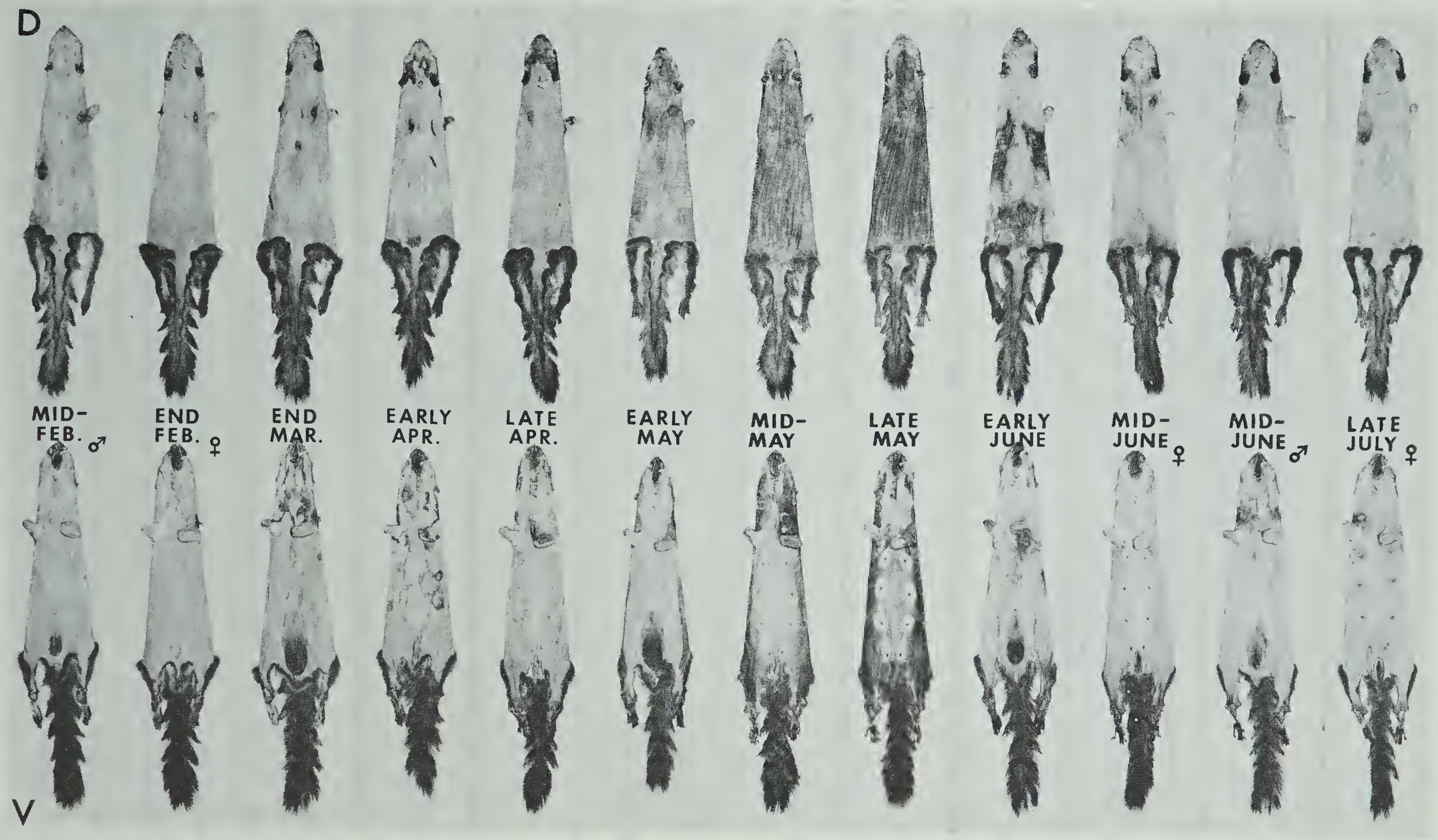


FIGURE 27 .SEQUENCE OF THE SPRING MOLT AS REVEALED BY PRIMING PATTERNS OF RED SQUIRREL PELTS

with full growth of summer pelage finishing over the ribs and finally at the base of the tail. Hair lost around the nipples of lactating females in late May, however, was not replaced until mid-summer. The tail did not molt with the rest of the body in spring.

During the summer months, juvenile squirrels experienced a light and rather rapid change from the soft juvenile pelage to adult summer fur. The pattern of hair growth closely followed the spring molt pattern, but apparently was not accompanied by hair loss. In late July it began over the crown, along the side stripes and over the dorsal surface of the forefeet. It progressed caudad over the back, the sides of the neck, the dorsal surface of the forelimbs and onto the flanks, to end on the chest and belly in mid-August. New hair grew in slowly on the hind limbs as these changes progressed. By the time the juvenile pelage growth was complete, all squirrels were showing heavy molt on the dorsal surface of the tail. Toward the end of August, this began to progress onto the lower back and included all of the tail pelage, marking the beginning of the fall molt.

The fall molt, illustrated by representative pelts as that of spring, appeared to progress much more rapidly and in the opposite sequence (Figure 28). As noted, molt had already progressed to the ventral surface of the tail and onto the back by the first week of September. Molt was complete over the lower back and up the dorsal mid-line of the thorax by mid-month, and at the end of September the shoulders, flanks, outer hind limbs and nape of the neck showed new pelage. The area of fur growth moved onto the central belly during the first week of October and by mid-month included all areas but the perineum, the axilla and inner forelimbs, the chin and throat,

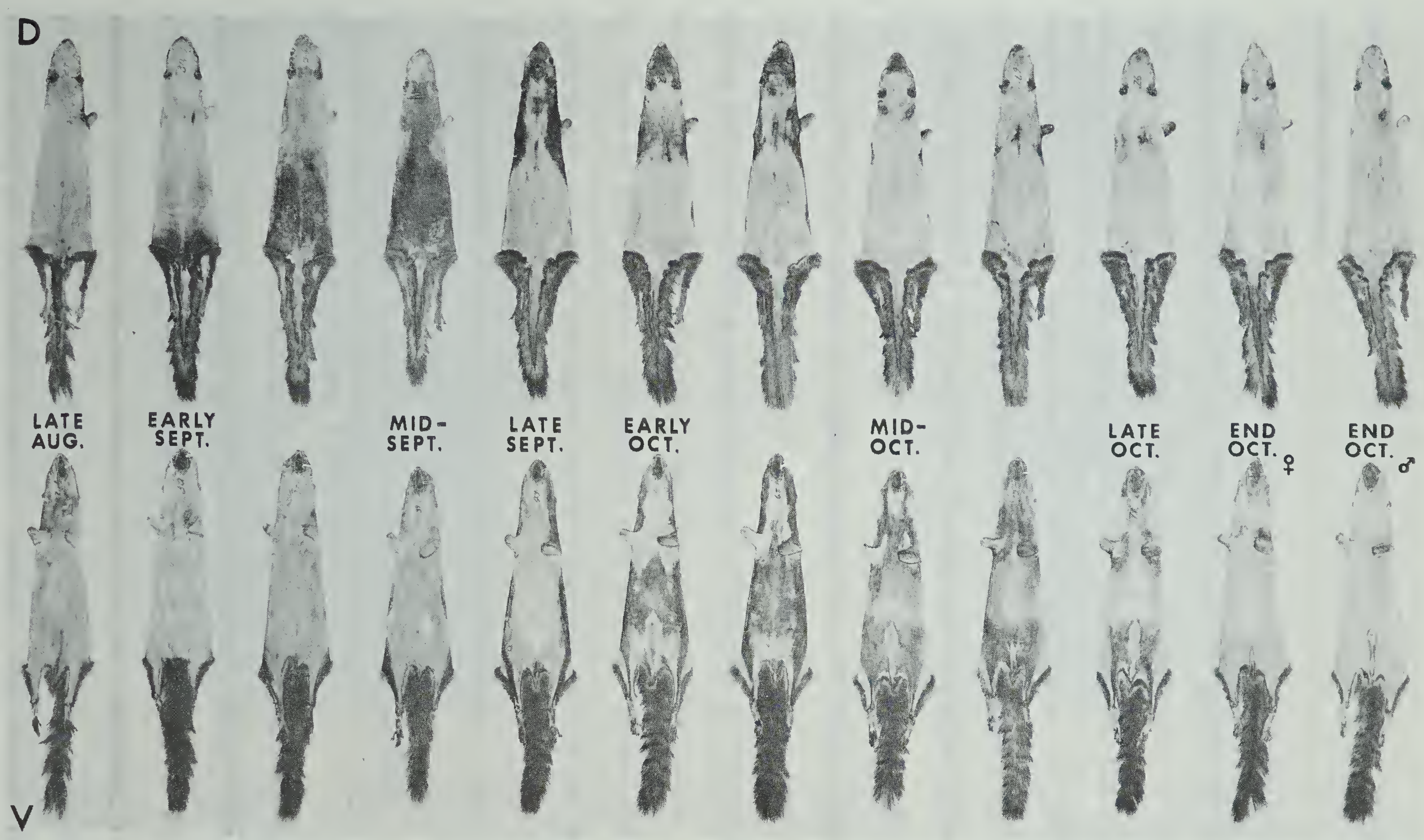


FIGURE 28. SEQUENCE OF THE FALL MOLT AS REVEALED BY PRIMING PATTERNS OF RED SQUIRREL PELTS

and the fore and hind feet. Molt was complete over these areas by the end of October.

Miscellaneous notes on pelage and pelt condition revealed two seasonal irregularities possibly important in the ecology of the red squirrel. During the breeding season many squirrel pelts of both sexes showed bite marks, appearing as two tiny holes in the skin corresponding to the incisor teeth of other squirrels. On females, however, bites were often so numerous and thickly spaced over the shoulders and nape of the neck that they were accompanied by heavy bruising and hair loss (Figure 29). These wounds were evidently inflicted by male squirrels during copulation. The other irregularity occurred during the summer months, when swarms of biting insects were one of the most striking characteristics of mid-day in the boreal ecosystem. Many squirrels were covered by buises which could be traced to this source. Apparently made by black flies, the marks appeared as pea-sized red spots around a puncture dot on the pelt side of the study skins (Figure 30).

II. Ecology of the Local Population

A. The winter study: Fall 1968 through Spring 1969

Temperature, Snow and Trapping Success:

Trap-success declined with the advent of freezing temperatures in early winter, then remained approximately constant until temperatures averaged about -20°F., below which there were almost no squirrels captured (Table 2). In late winter, captures per trap-hour increased as temperatures rose above -20°F., then above 0°F., but decreased again during the cold spell in March. However, trap success failed to

FIGURE 29 .RED SQUIRREL IN SPRING - FEMALE SHOWING HAIR LOSS ON BACK

FIGURE 30 .RED SQUIRREL SUMMER PELT WITH BLACK FLY BITE MARKS

October				November				December				January			
Males		Females		Males		Females		Males		Females		Males		Females	
Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.
6	5*	1	3*	6	5*	1	3*		5*	1	3*		5*		3*
11*	13	7*	4	11*	13	7*	8			15*	8				8
		15*	8		17	15*	12				12				
			10*				14*				14*				
			12				16*								
			14*												
			16*												

February				March				April				May			
Males		Females		Males		Females		Males		Females		Males		Females	
Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.	Ad.	Juv.
	5*	1	3*	18	5*	1	3*	23	5*	1	3*	23	5*	1	3*
		15*	4		13	15*	4		13	15*	4		13	15*	4
			8		21	20*	10*		17	20*	10*		22	20*	14*
			10*				14*		22		12		24	33	16*
			12				16*		24		14*		25		30
			14*						25		16*		26*		32*
			16*										27		
													28		
													31*		

* = age confirmed by examination of cheek tooth wear

TABLE 2: Sex and age of individual red squirrels recorded on the study plot - October 1, 1968 to May 31, 1969

respond as expected to the sudden warming in April. A preliminary increase with rising temperatures early in the month was followed by a great decrease in captures per hour as temperatures rose substantially above freezing and movement on the ground was inhibited by melt-water. The capture rate began to increase again slowly through May.

Trapping Success and Home Ranges:

Through the period October 1968 to May 1969, 30 different squirrels were marked and released on the study plot. Few were present over the entire eight months and all displayed changes in areas of home range, sometimes moving entirely off the study area for periods of time. A month by month account of these changes follows, illustrated by Figures 31 to 38 and by Tables 2 and 3.

The number of squirrels using the plot varied over the months of study (Table 3). A fluctuation from 14 in fall to 3 in mid-winter and to a high of 20 with the influx of breeding transients in spring suggests that carrying capacity may be a far more complex principle than has previously been imagined, at least in areas of harsh climate.

Home range size declined sharply from October to November with the onset of sub-freezing temperatures, reflecting the decline in trapping success previously mentioned. The end of the period of restricted movement in mid-winter was marked by an equally sharp increase from February to March. The continued increase in size in April and May, to values exceeding those in October, could be attributed to increased activity associated with mating, and possibly also to greater (arboreal) movement necessary in foraging over inundated ground, larger foraging areas available with a lower spring resident population, and an increasing number of daylight hours.

	No. of Squirrels Recorded	Est. Mean Range Area (acres)	Per Cent Landscape Type Occupied O D	S-O D	S-O W	D W	Total	No. of Occupied Middens	No. of Captures per Hour x 10^3 (10-day means)
1968									
October	14	2.9	62	54	60	78	64	6	183[1], 701, 641
November	13	0.6	0	13	25	41	18	5	420, 231, 167
December	7	0.4	0	2	9	12	5	6	100, 250, 133
1969									
January	3	0.2	0	0	3	5	2	3	0[2], 21, 33
February	10	1.6	1	19	37	33	24	5	31, 191, 157
March	12	3.1	23	35	46	66	42	3	531, 338, 346
April	16	3.9	21	65	46	56	47	5	529, 270, 246
May	20	3.9	33	67	50	60	52	7	315, 418, 344

1 - beginning of program, squirrels unaccustomed to traps

2 - only 4 days trapped

TABLE 3: Summary of trapping results - October 1, 1968 to May 31, 1969

The percentage of each landscape type occupied over different months likely reflects habitat preferences. Open dry areas were essentially deserted over the period of extreme cold (Table 3), probably because they offer little food, shelter or soil for burrowing even at the warmest times of year, and the icy wind-blown snows likely present a greater barrier to tunnelling than the lighter snows of other areas. The much greater use of this habitat in fall than in spring may have been due to avoidance of defended ranges by dispersing juveniles, or simply to chance and the small size of open dry areas. Of the three remaining landscape types, the more dense and wet areas seemed to be preferred from fall until the onset of thawing temperatures in spring. The change to greater use of the semi-open dry habitat at this time was apparently due to accumulation of water from melting snow in the other two landscape types.

The distribution of midden sites also reflects a generally greater attraction to the dense wet landscape type, with five of the seven middens in that region and one each in the semi-open wet and semi-open dry areas. This attraction is apparently to areas of deeper soil, more favorable for burrowing, as well as to areas where dense vegetation gives maximum protection from wind to permit accumulation of low density, highly insulative snow. Occupation of these middens seemed rather variable, but it can be noted that the one between traps D-2 and 3, in the semi-open dry region, was not occupied until the spring melt when the wetter areas presumably became unfavorable.

The proportion of the plot that was used each month declined in mid-winter and increased again in spring (Table 3). At maximum contraction only about two per cent of the plot was used. This was a

30-fold decrease from the amount used in October and is the same order of magnitude as the winter range contraction of large ungulates. Although in May there were more squirrels on the plot and the home ranges of residents were larger, less of the plot was used than in the previous autumn (Table 3). This apparent inconsistency is easily explained. Of the 20 squirrels recorded on the plot in May, 8 were clearly transients. Therefore, the number of May residents was less than the number of October residents. Furthermore, part of the plot was covered by melt-water and hence essentially uninhabitable.

Movements:

In October there was little sporadic movement away from centers of activity and out of home ranges except in the case of No. 3 (Figure 31). Its home range was apparently limited to 1.5 acres, much smaller than expected, by the proximity of centers of activity of Nos. 6 and 15.

In November considerable reduction of movement resulted in the disappearance of Nos. 4 and 10 from the periphery of the plot (Figure 32). Also, following the death of No. 11 in a trap on November 7, No. 3 immediately moved from its October center of activity to occupy the newly vacant midden. Further changes in November included the movement of No. 15 during the first week to a new midden just south of the plot boundary; the disappearance of No. 7 from its midden 400 feet east of the plot around mid-month and its replacement by No. 16, a squirrel which had previously lived in a rock crevice between Nos. 7 and 13; and the disappearance of No. 6 late in the last week. Several sporadic movements occurred and were apparently directed toward areas originally occupied by Nos. 7 and 11. The single capture of a new squirrel, No. 17, was likely also the result of a sporadic movement from a center of activity east of the plot.

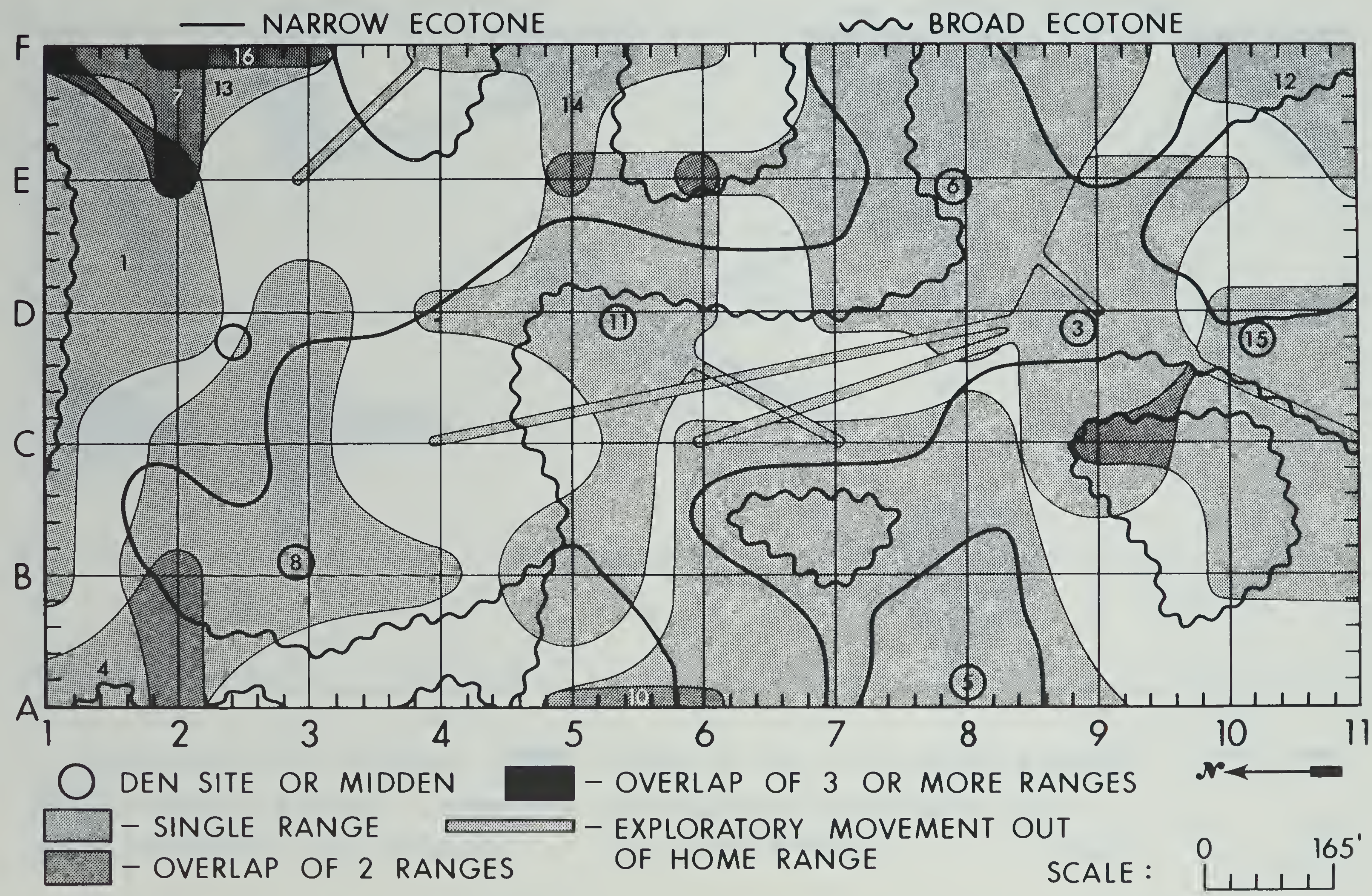


FIGURE 31 · MOVEMENTS AND HOME RANGES - OCTOBER

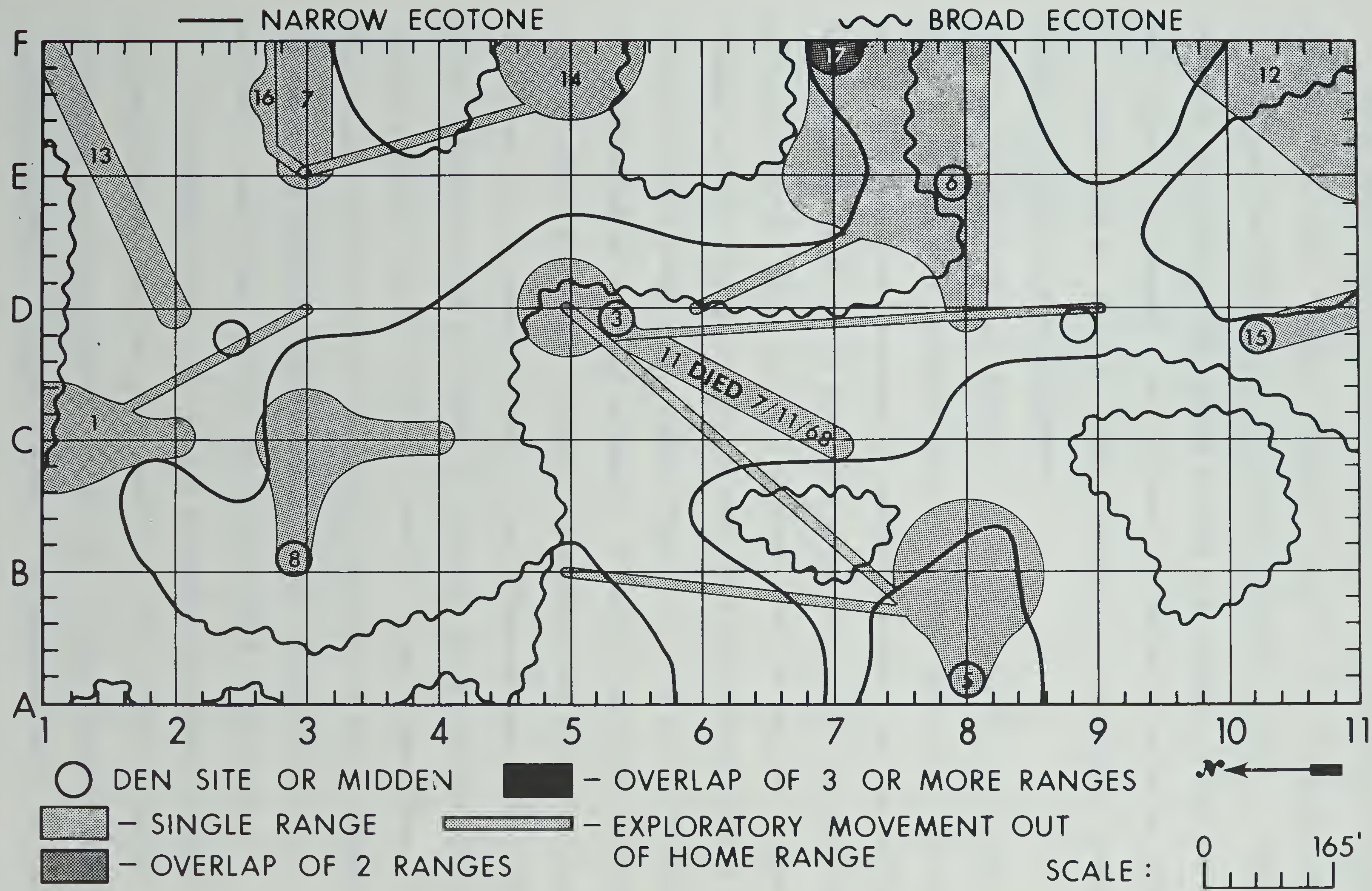


FIGURE 32 . MOVEMENTS AND HOME RANGES - NOVEMBER

In December there was still shifting in the position of mapped ranges (Figure 33). Between December 12 and 14, No. 3 was apparently chased from, and replaced on, the midden near D-5 by No. 5. Number 3 moved to the newly vacant midden at trap D-8. Number 15 was captured only twice, on December 4 and 16, near the midden occupied in October. Its tracks were not recorded during the rest of the month. Sporadic movement movement was not observed.

In January there was almost no activity above the snow, with Nos. 3, 5 and 8 each captured only once (Figure 34). Short distances in dense forest were traversed by permanent trails over the shallow snow between trees or by use of snow-free areas under logs. However, the deep, soft taiga snows inhibited movement over the surface in most areas, and cone stockpiles were reached by intranivean tunnels at the level of dense, older snow. Heavy deposits of snow on the branches of trees prevented arboreal movement. Evidence from track and snow tunnel surveys suggested that squirrel activity was almost entirely restricted to the immediate area of the midden and nearby cone stockpiles. Careful surveys along the lines of the grid, which now consisted of packed snow-shoe trails, failed to disclose signs of any other squirrels. There was no movement onto the plot by squirrels on nearby middens, and apparently no sporadic movement or attempted shifts in centers of activity, even though four of the seven middens were vacant.

In February there was a marked increase in activity and many squirrels living near the plot (Nos. 1, 4, 10, 12, 14, 15 and 16) reappeared in the trap record (Figure 35). Three squirrels changed their centers of activity: Number 4 moved to a temporary den in a rock crevice near trap C-2 early in the month, No. 5 moved back to the

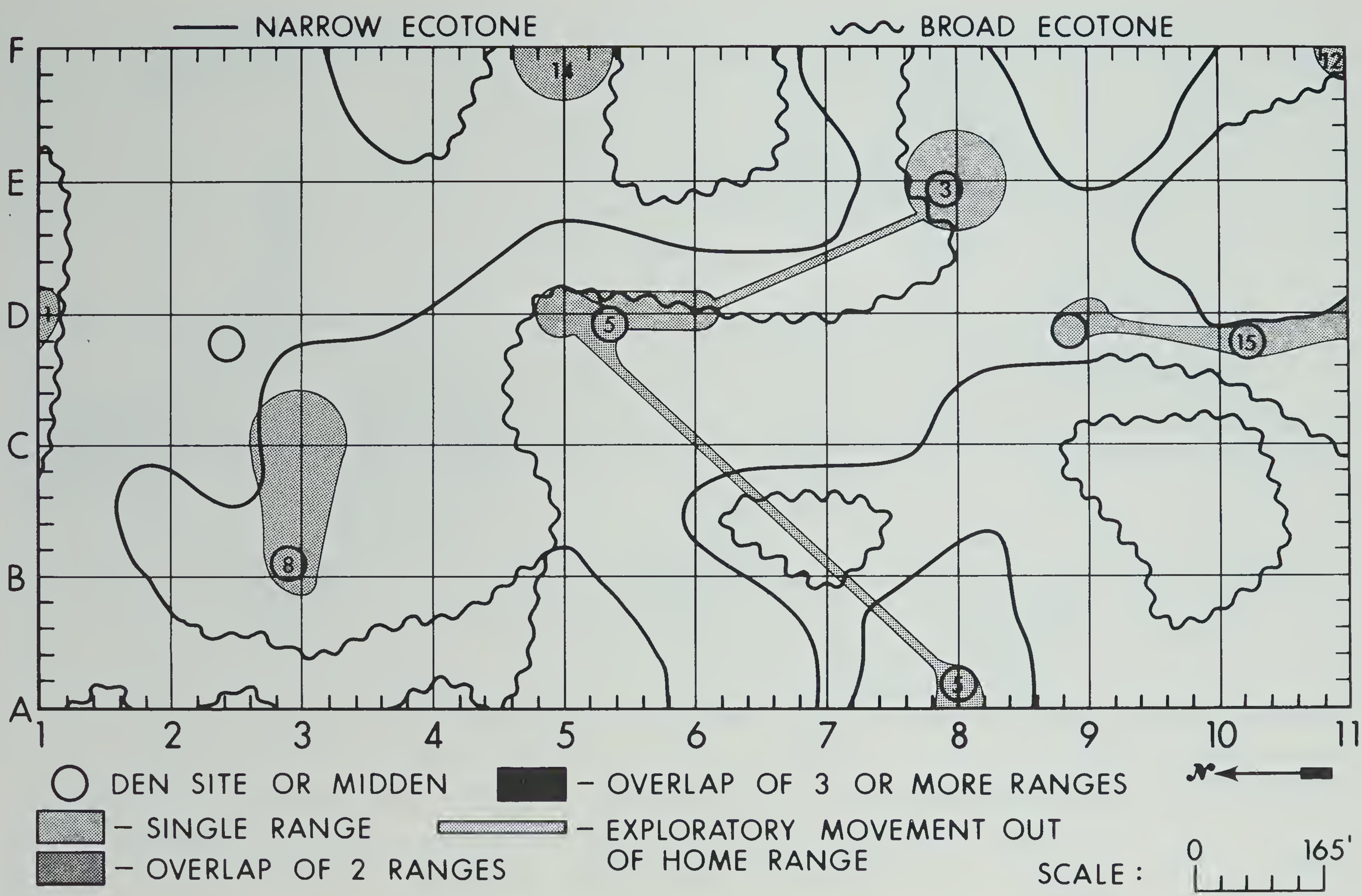


FIGURE 33 . MOVEMENTS AND HOME RANGES - DECEMBER

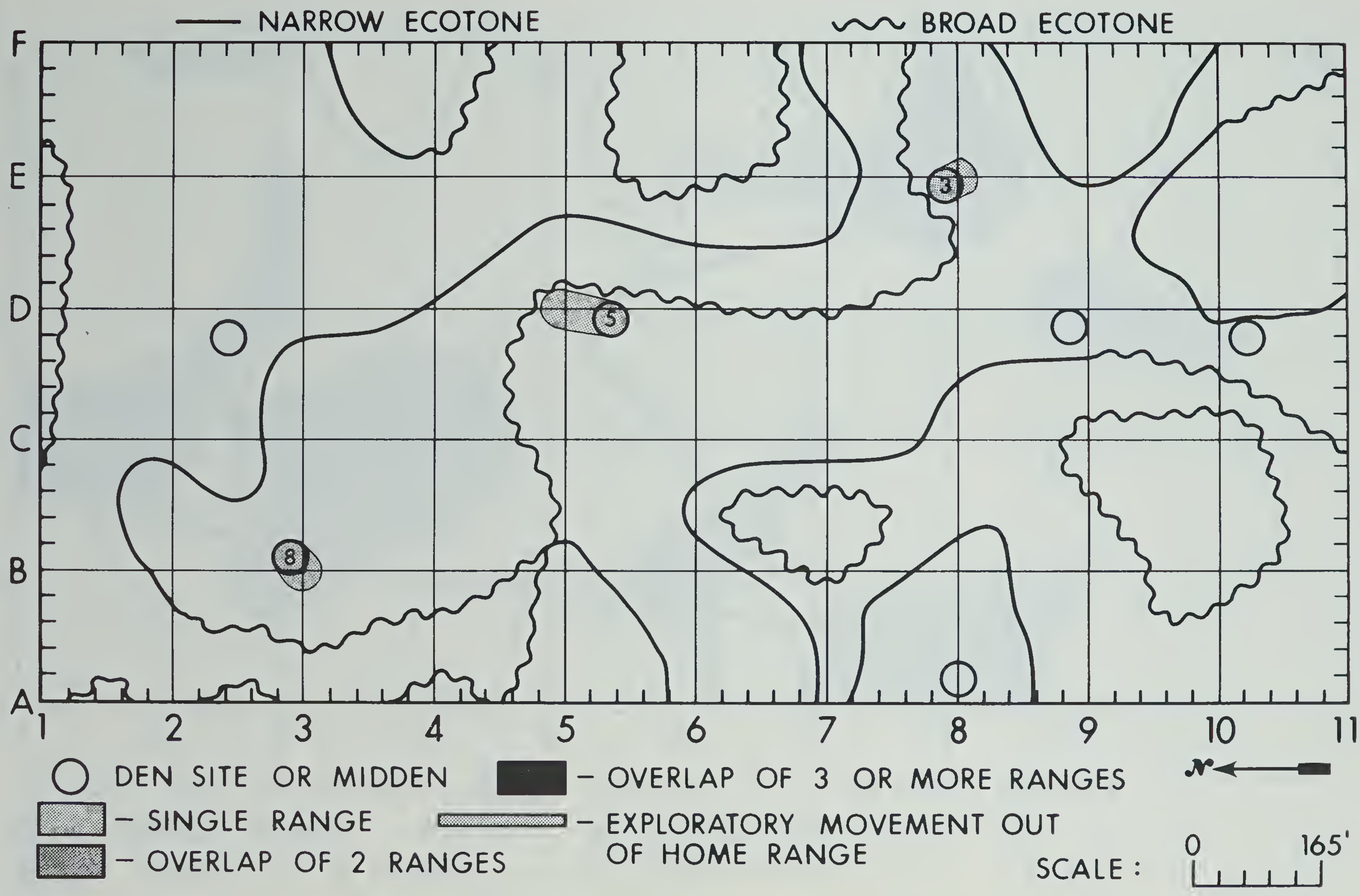


FIGURE 34 · MOVEMENTS AND HOME RANGES - JANUARY

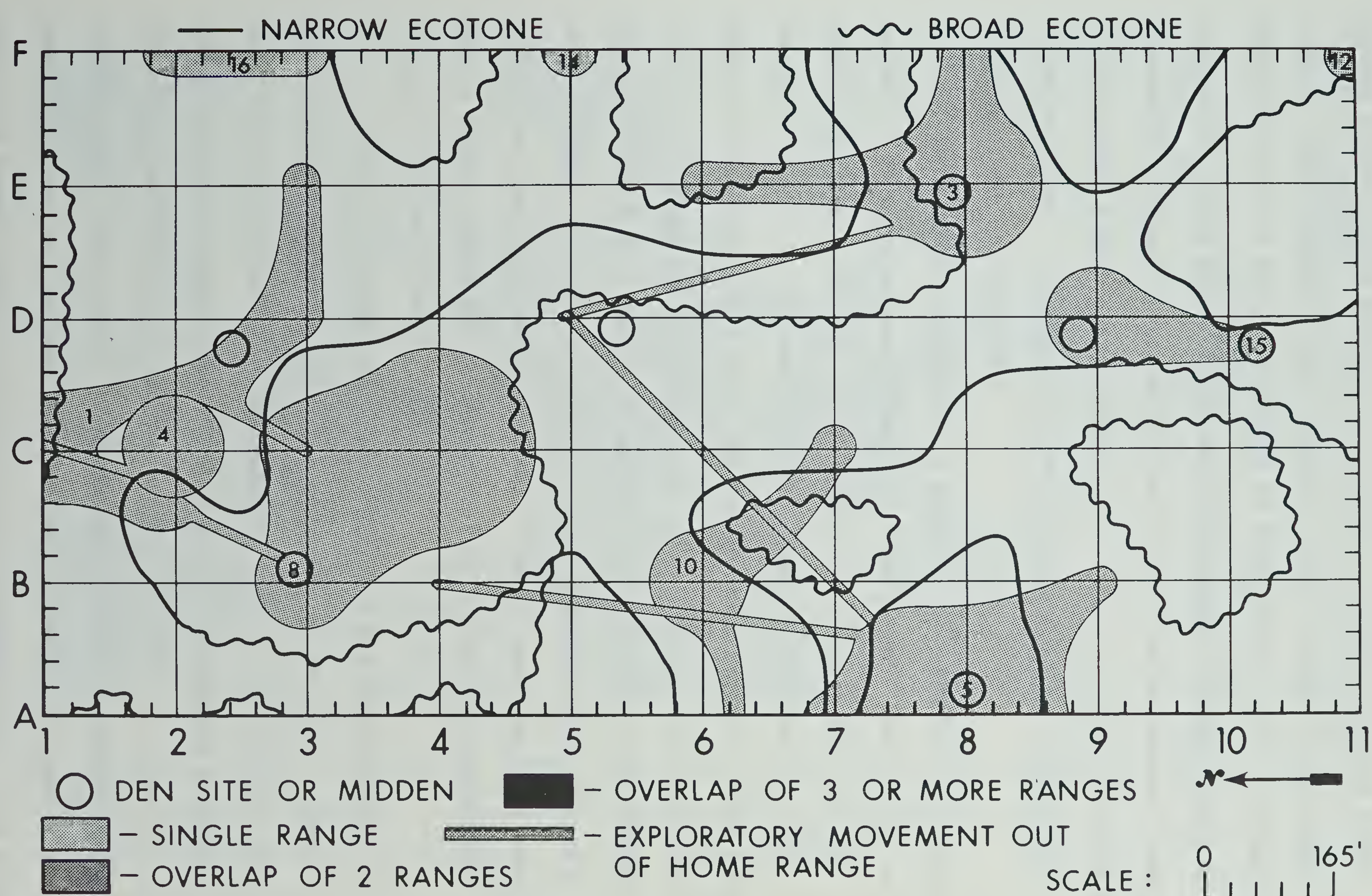


FIGURE 35 . MOVEMENTS AND HOME RANGES - FEBRUARY

midden at A-8 around February 19, and No. 15 moved back and forth several times between middens near D-9, D-10 and off the plot some 200 feet south of D-11. According to track records, No. 15 spent most time at the third site. There was some sporadic movement, most of it apparently related to the relocation of No. 5 and subsequent investigation of the vacant midden near D-5 by No. 3. Finally, in the last few days of February, No. 8 disappeared from the plot and No. 4 immediately moved onto the vacant midden.

In March, further increase in activity was apparent from the greater number of sporadic movements recorded (Figure 36). Some shifts in range were noted: Number 3 moved back to the midden near D-5 on March 8, No. 15 was apparently active south of the plot all month except for one capture at D-8, and No. 16 moved north onto the range of No. 13. Three new squirrels, Nos. 18, 20 and 21 were recorded during March, probably as a result of sporadic movement from some distance away. Numbers 18 and 21, both males, were captured only once each during the study period, but No. 20, a female, had apparently moved onto a vacant midden 600 feet west of trap A-4 and was recaptured regularly in the following months.

In April, a further increase in activity was noted (Figure 37). More changes occurred in the range structure of the plot: Number 3 moved back to the midden at E-8 again on April 4 and remained there for the rest of the study period; Nos. 10 and 12 disappeared suddenly from the trap records about mid-month; and No. 13 moved to a rock-crevice den farther west, away from No. 16 whose range expanded tremendously and overlapped some of the home range of No. 4. Number 1 appeared to have moved its range slightly north, but still occupied much of the same

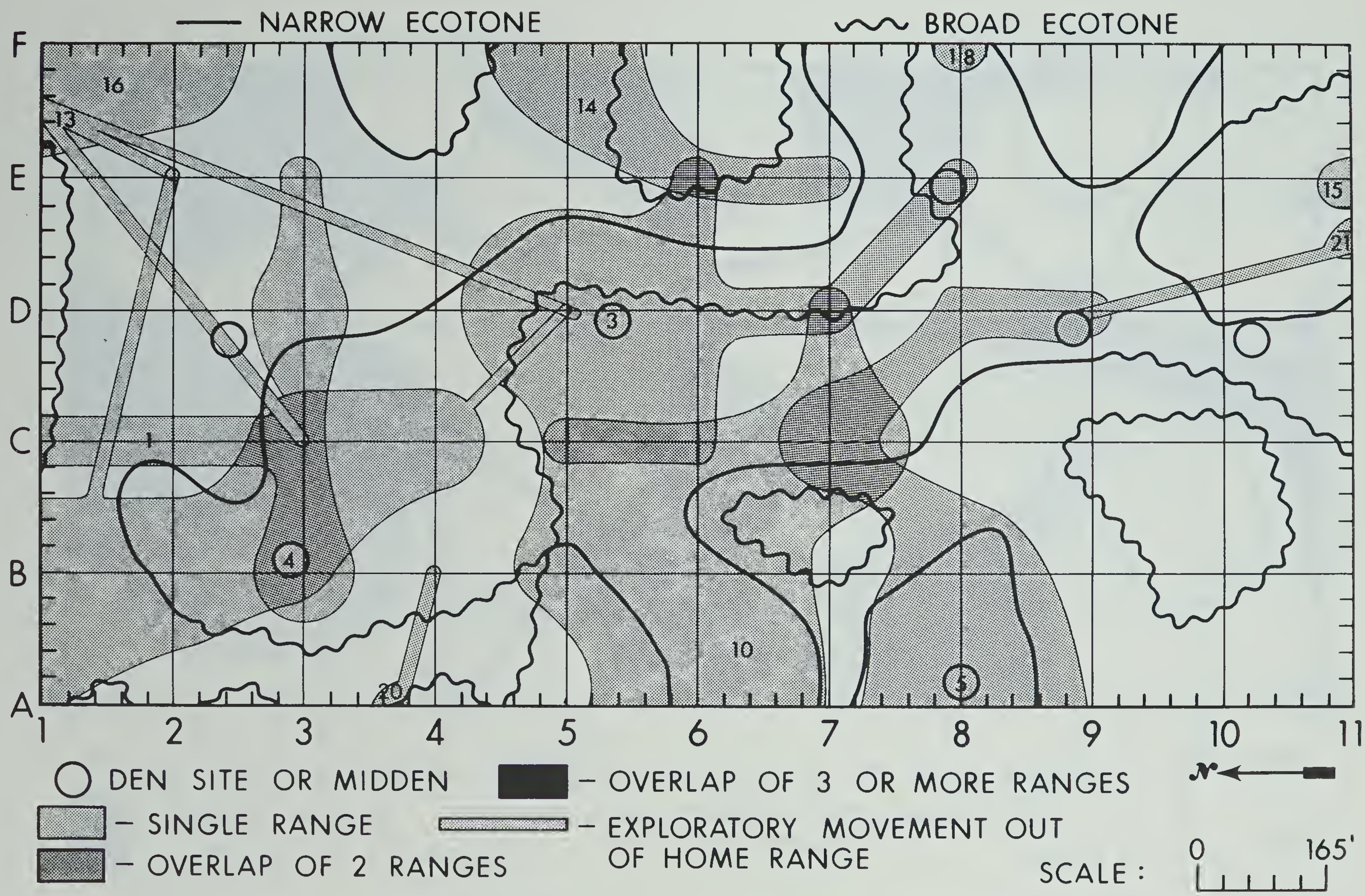


FIGURE 36 · MOVEMENTS AND HOME RANGES - MARCH

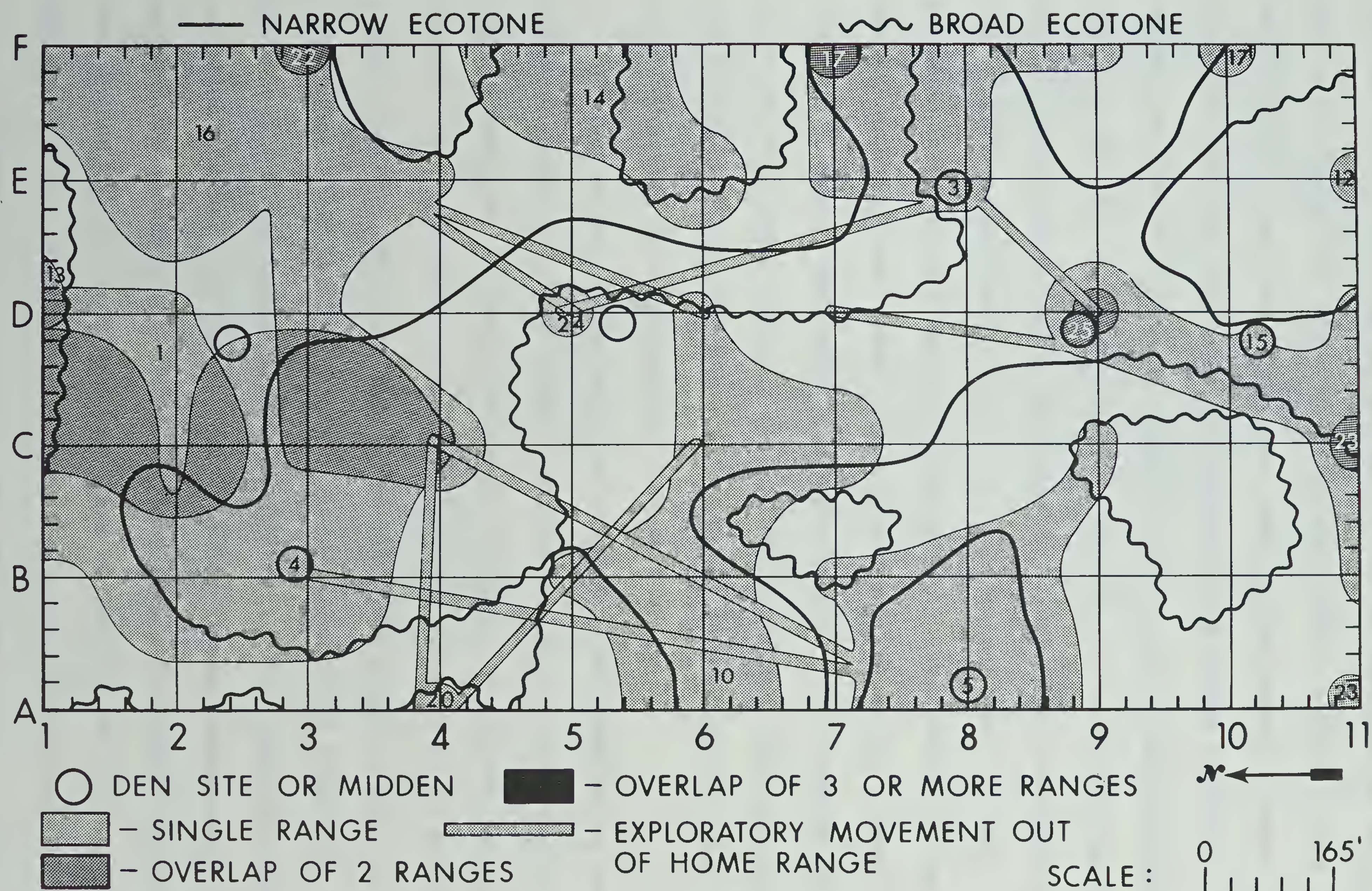


FIGURE 37 . MOVEMENTS AND HOME RANGES - APRIL

area as No. 4. Four new males (Nos. 22 to 25) appeared on the plot in April, all except No. 22 in the final two weeks. Number 23 was captured twice, and the others only once in that month. Number 24 was taken in trap D-5, but apparently moved to the midden between D-2 and 3 around the end of the month. Number 25 was captured near the vacant midden at D-9 on the area defended by No. 15, the latter having moved back to the midden at D-10. An unmarked male took up residence at trap D-5 on or just before April 27. This animal (No. 26) was extremely trap-shy and was not captured until May. Number 17 was taken once, its first record since November. Number 20, a female first recorded in March, was recaptured three times. These records appeared to be due to a great increase in sporadic movements, particularly in the last half of the month and coinciding with the onset of the breeding season for squirrels in the study area.

May was primarily the month of pregnancy, although mating was still going on during the first week. Activity on the plot was similar to that in April but without such a high incidence of sporadic movement (Figure 38). Capture of seven new squirrels (Nos. 26 to 33 inclusive) brought the total to 20 in the May record, with eight of these not reappearing after that month and therefore considered transients. Numbers 22 and 23, males taken first in April, were captured twice in early May and were not taken again. Number 25 was unsuccessful in maintaining occupancy of the midden near trap D-9, apparently having been chased No. 15 north into the areas of Nos. 24 and 32. It then disappeared from the plot. Number 26 was captured only three times, but was sighted almost every day over the midden near D-5. Males No. 27, 28 and 32 were captured only once, in the first week of May.

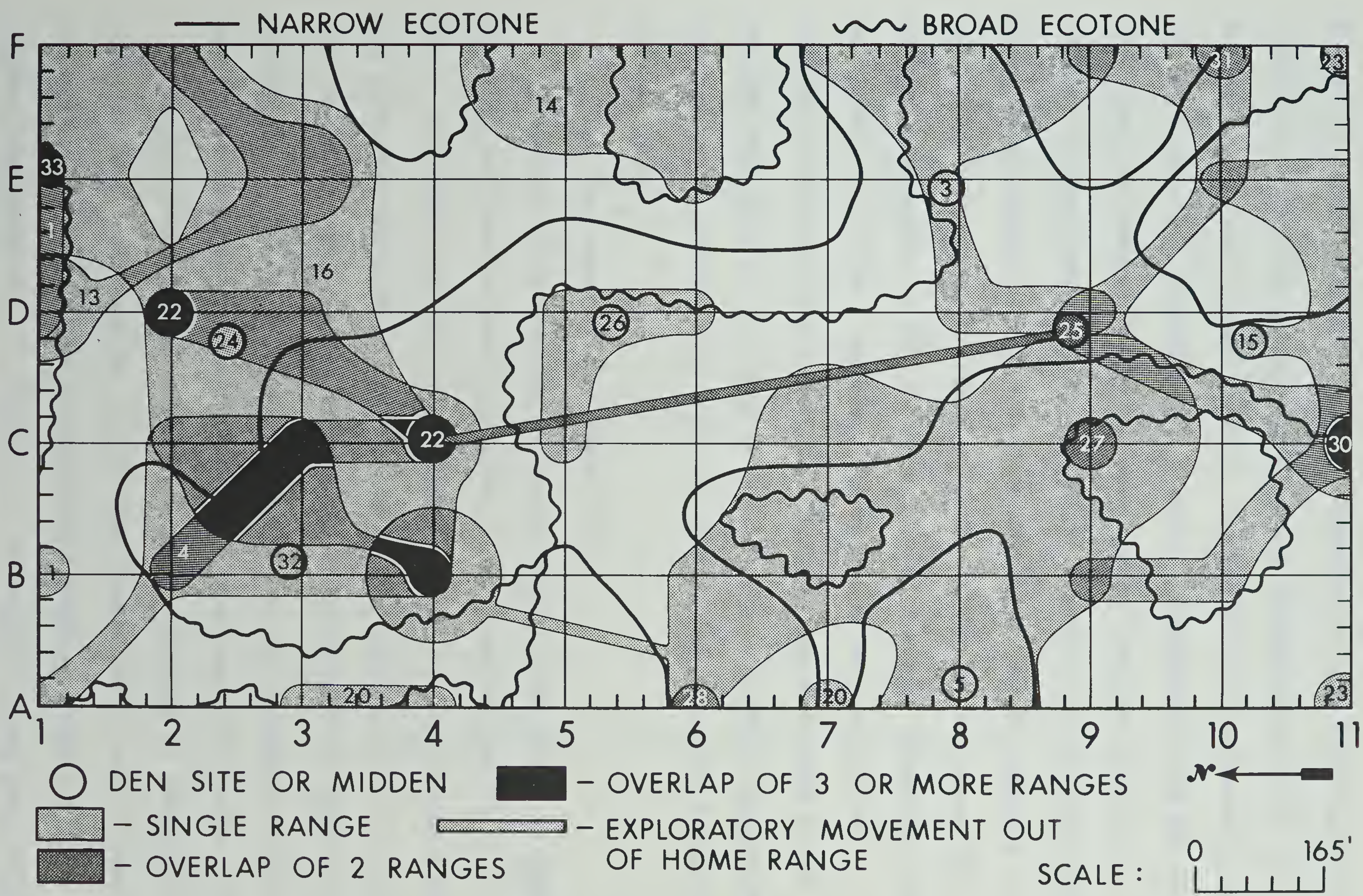


FIGURE 38 . MOVEMENTS AND HOME RANGES - MAY

Number 31 later apparently took up residence 60 feet south-east of trap F-11 to fill the vacancy left by the disappearance of No. 12. Numbers 30, 32 and 33 were females. Number 32 moved permanently onto the plot near B-3, replacing No. 4 which disappeared around May 10. The other two females likely had moved nearer the plot over the winter, as they were present frequently in summer trap records after their first capture in May. Extreme overlap of ranges observed on the north end of the plot was eased with the disappearance, apparently through emigration, of No. 4 on May 10, No. 1 around mid-month, and No. 13 at month's end. However, the ranges of male No. 24 and females No. 16 and 32 continued to overlap, largely because of the extreme expansion of the range of No. 16. It is perhaps significant that these two females were the only ones on the plot that failed to produce young.

B. The summer study - Summer 1969

Results of live-trapping on the study plot from June 1 to August 31, 1969 are given by month in Tables 4 and 5 and Figures 39 to 43. Adult (including yearling) red squirrels occupying significant areas of the plot were males No. 5, 24, 26 and 32, and females No. 3, 14, 15, 16, 20 and 32. The females were killed at the end of the summer to accurately determine age, reproductive status and fecundity (Table 6), and show relationships between these and behavioral differences noted.

In June there was no record of sporadic movement by residents of the plot, but transients No. 21, 25 and 35 were noted still trying to relocate after the territory upset during breeding (Figure 39). Further, squirrels No. 17, 18, 30, 33, 34 and 36, living near the plot but not often trapped, may have been taken while on exploratory forays

June				July						August					
Males		Females		Males			Females			Males			Females		
Ad.	(Yearl.)	Ad.	(Yearl.)	Ad.	(Yearl.)	Juv.	Ad.	(Yearl.)	Juv.	Ad.	(Yearl.)	Juv.	Ad.	(Yearl.)	Juv.
18	5*	1	3*		5*	41	15*	3*	37	34*	5*	42	15*	3*	37
34*	17	15*	14*		24	42	20*	14*	38		24	43	20*	14*	38
	21	20*	16*		26	43		16*	40		26*	46	33	16*	40
	24	33	30		31	44		32*	45		31*	48		32*	45
	25		32*			46		36	47			50			47
	26*		36			48			53			51			53
	31*					50						52			54
	35					51						57			55
						52									56
															58

* = age confirmed by examination of cheek tooth wear

TABLE 4: Sex and age of individual red squirrels recorded on the study plot - June 1 to August 31, 1969

1969	No. of Squirrels Recorded Ad.	Juv.	Est. Mean Range Area (acres) Ad.		Juv.	Est. Per Cent Juv. area co-occupied by mother	Per Cent Landscape Type Occupied O D	S-O D	S-O W	D W	Tot.	No. of Occupied Middens	No. of Captures per Hour x 10^3 (10-day means)
June	10 ♂♂	0	3.5 (#5, 24)	♂♂	- -	-	21	47	65	51	48	8	302, 329, 373
	10 ♀♀	0	2.8 (#3, 15)	♀♀	- -								
July	4 ♂♂	9	5.2 (#5, 24)	♂♂	0.8	81	53	75	77	68	70	7	303, 619, 667
	7 ♀♀	6	7.5 (#3, 15)	♀♀	1.1								
August	5 ♂♂	8	4.8 (#5, 24)	♂♂	1.0	15	49	80	53	64	65	7	613, 520, 464
	7 ♀♀	10	3.4 (#3, 15)	♀♀	2.6								

TABLE 5: Summary of trapping results - June 1 to August 31, 1969

Female No.	Age in years during summer 1969	Corpora Albicantia	Placental Scars	Size of Litter	Individuals in Litter
3	1	5	4	3	(45, 47, 50)
14	1	5	5	5	(37, 40, 44, 46, 53)
15	3	5	5	5	(38, 42, 43, 51, 52)
16	1	0	0	0	
20	3	5	5	?	(41, 48, 54 ..)
32	1	3	3	0	

Other females near the plot and which were known to have had young were: Nos. 1, 33 and 36.

Females known to be living somewhere near the plot and which may have had young were: Nos. 8 and 30.

TABLE 6: Reproductive data from female red squirrels recorded on or near the study plot in summer 1969

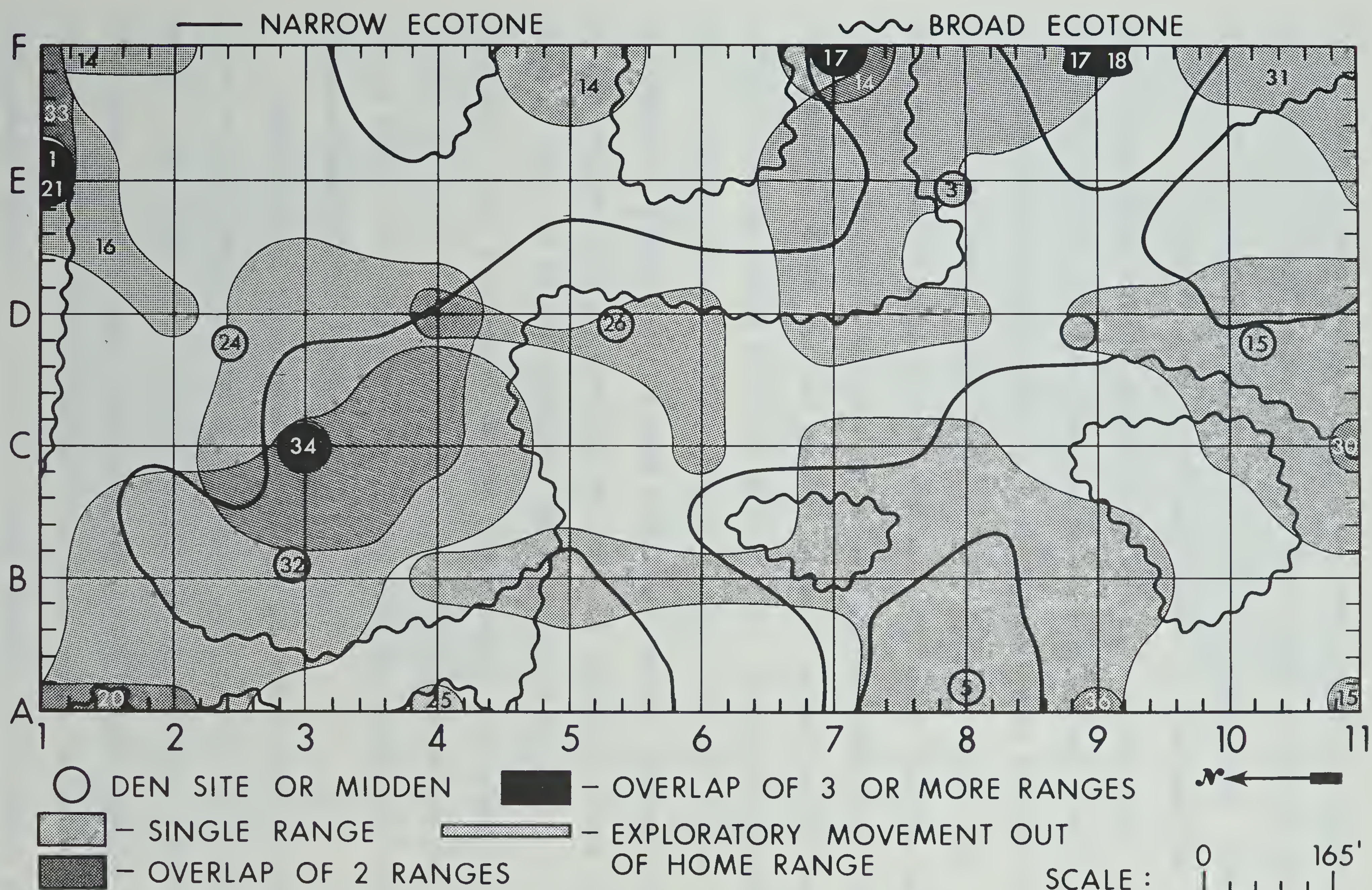


FIGURE 39 . MOVEMENTS AND HOME RANGES - JUNE

out of their normal ranges. It appeared that a slight reduction in activity, and possibly also in size of home ranges of females with young, had occurred from the May values of the winter study. The June reduction in captures per hour was expected due to the cessation of sporadic movement and the consolidation of ranges on the plot. In lactating females this consolidation seemed more extreme than in males or nulliparous females, with most activity confined to the area of their nest and young. This likely accounts for most of the June difference in home range size between male and female squirrels shown in Table 5. Reduction in the range of nulliparous female No. 16 was not similarly caused, but was apparently due to social conflict with either lactating female No. 14 or male No. 24. It must be cautioned that although estimates of home range size given in Table 5 were considered reliable enough to show significant trends, extreme variation between squirrels of the same age and sex (e.g. males No. 5 and 26) prevent wider use of these values. The only change in center of activity in June occurred at the end of the month, when lactating female No. 1 disappeared from the heavily populated area just north of the plot. This female was seen later, with her litter, at a new location some 500 feet north west of trap A-1.

Capture of the first juveniles on July 10 marked a sudden change in activity on the plot, with a doubling of captures per hour (Table 5). Females with young at this date showed a two-fold increase in size of home range, but home range size for males and nulliparous females seemed to remain much the same and still with extreme variation between individuals (Figure 40). The only change recorded in the latter group was an increase in the area occupied by No. 24, a male which had entered

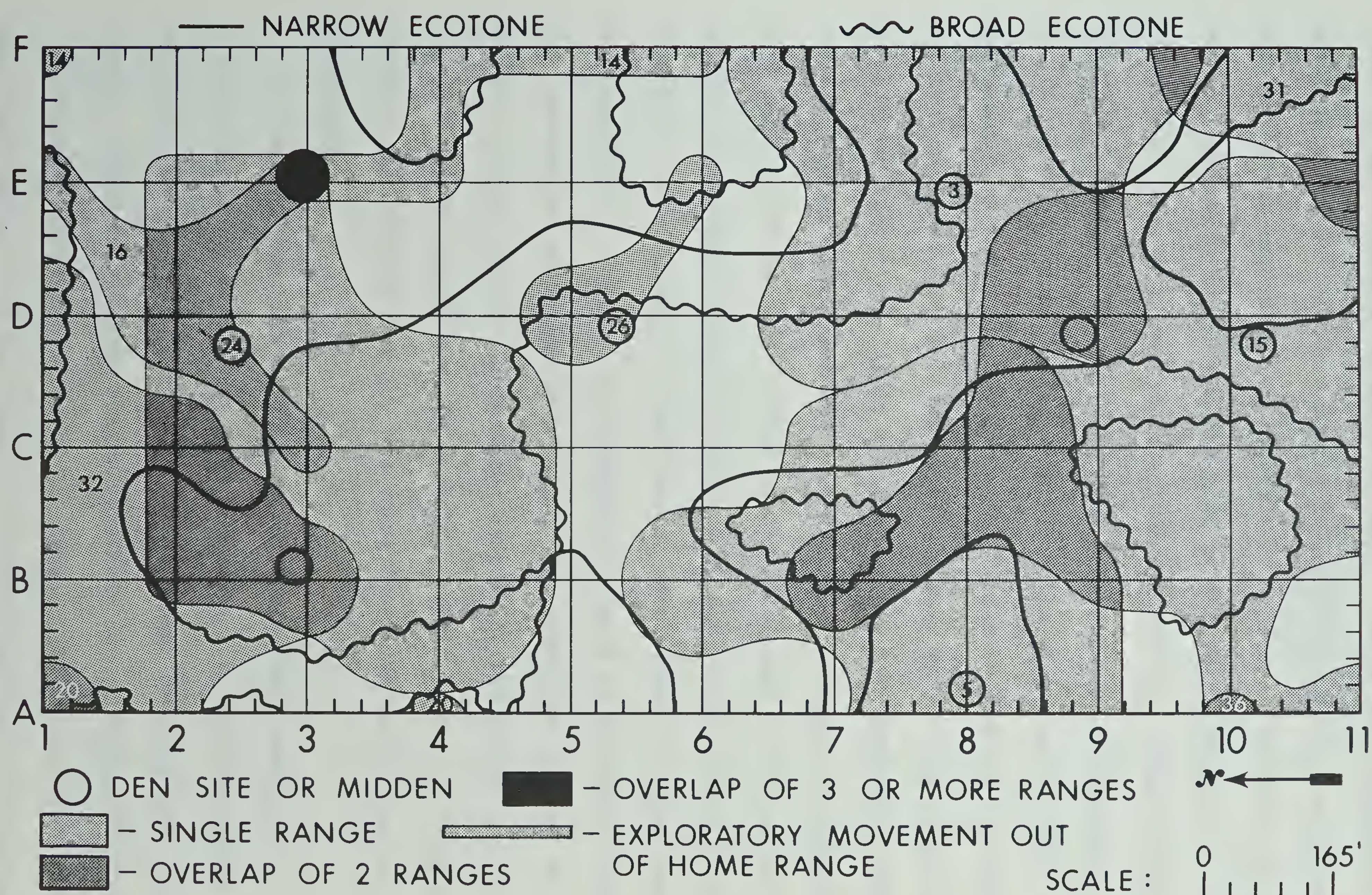


FIGURE 40 · MOVEMENTS AND HOME RANGES (Adults only) - JULY

the plot as a breeding transient in April. This range expansion was apparently due to intense activity in familiarization with the area, and the boundaries seemed rather unstable. Defense of the area was sufficient, however, to force No. 32 off the plot to the vacant midden of No. 1 around July 10. The loss of this female's litter, either through resorption or at birth, may also have been related to aggression by No. 24. With the intensified defense of the plot area in July, no transients were trapped, and lactating female No. 36 was the only squirrel recorded from a midden some distance away. The single capture of this individual was likely a result of the aforementioned general range expansion of all females with young. The ranges of juveniles were small, coherent and limited to areas defended by the mother or to adjacent unoccupied regions, resulting in the litter clusters shown in Figure 41. The ranges of young females were slightly larger than those of young males. Further, the frequent sighting of lactating females with certain of their female young, as No. 3 with No. 45 and No. 15 with No. 38, as well as the simultaneous capture of the latter pair on July 27, may be significant in revealing greater parental care for female young generally or for one young female in particular out of each litter.

In August, the most obvious change was a great reduction in size of home ranges of the females with young, back to values similar to those recorded in June (Figure 42). The ranges of males and nulliparous females seemed to withdraw slightly, likely due to border conflicts with the many dispersing young. For females No. 14 and 15, the August range and perhaps even the center of activity may have shifted away from those areas occupied in July and where juveniles were therefore

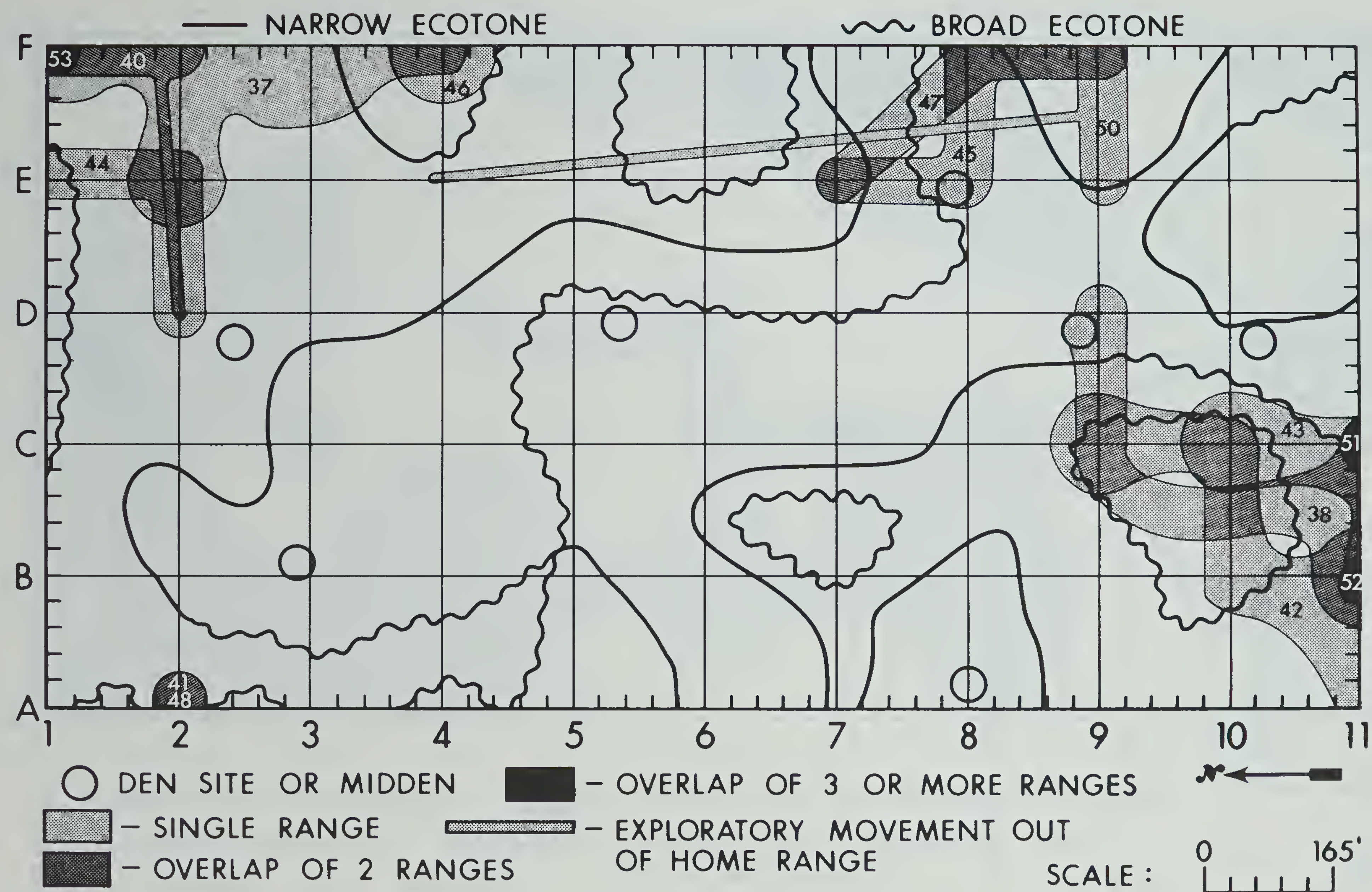


FIGURE 41 · MOVEMENTS AND HOME RANGES
(for Juveniles only) – JULY

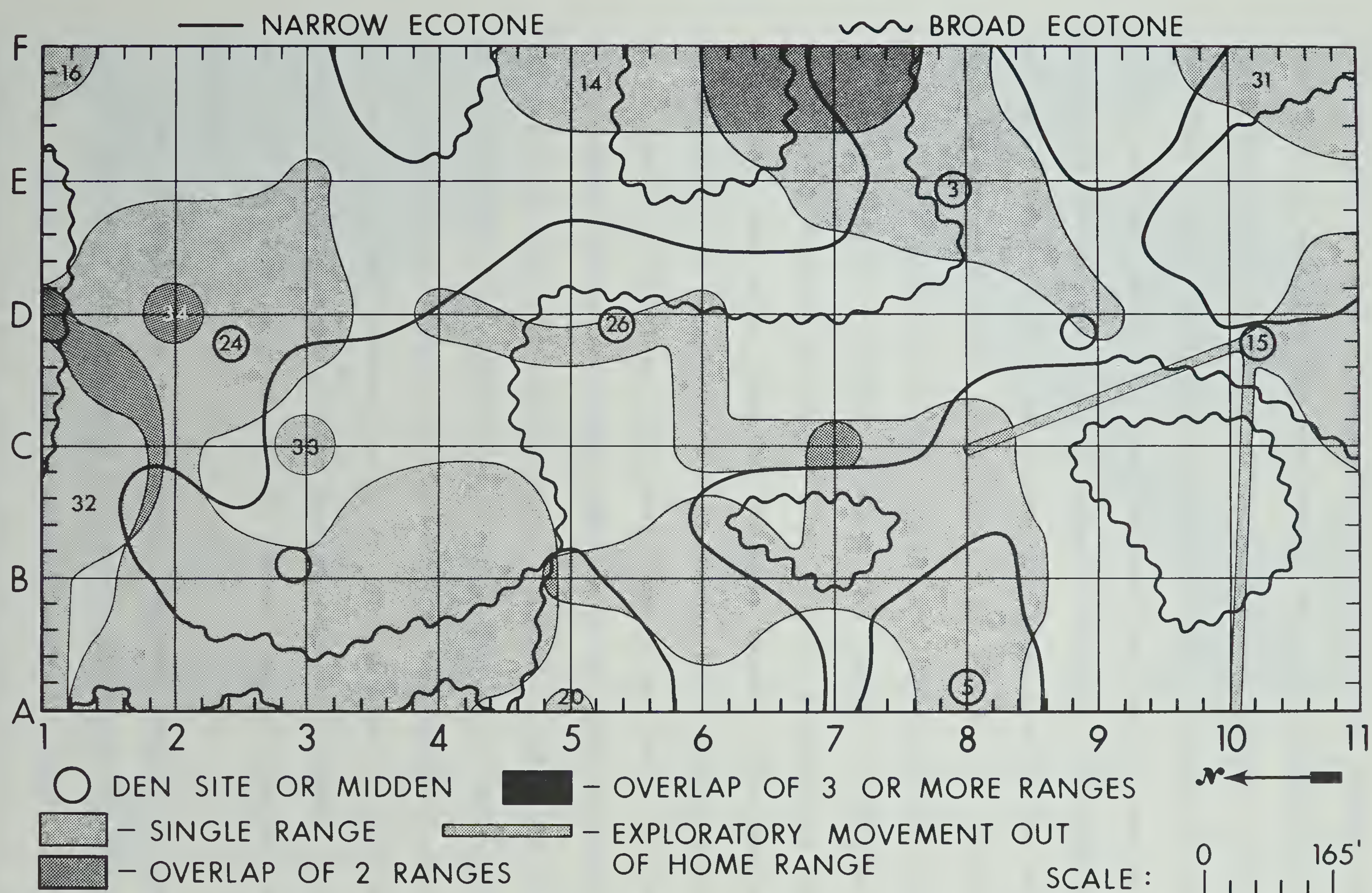


FIGURE 42 · MOVEMENTS AND HOME RANGES (Adults only) - AUGUST

concentrated. Occasionally captured individuals No. 33 and 34 were recorded, and may also have been moving, at least temporarily, from areas where border conflicts with juveniles were extreme. No other squirrels unusual in the trap record were taken. Number 36, present in June and July but living some distance from the plot was not recorded, apparently having contracted its range to the west. Captures per hour decreased through August, reflecting this range contraction, but remained much higher than in June due to the presence of dispersing juveniles. Considerable change from the July appearance was noted in the August ranges of juveniles (Figure 43). Those of juvenile females were greatly enlarged from their sizes in July, although the ranges of males, when measurable, were only slightly larger. This resulted in an almost three-fold difference in size of home range between the sexes of the juvenile age class. All young females recorded in July were still present in the same areas, and several new ones were observed attempting to establish territories on the plot. The juvenile females which had earlier apparently been favored, Nos. 38, 45 and possibly 37, had in August the largest, most coherent and best defended ranges. For juvenile males, however, two of the nine recorded in July had disappeared, many seemed to have changed areas of residence or showed very diffuse ranges with scattered captures, and only one new individual was taken.

Habitat utilization was also very changeable during the summer months, and after the beginning of juvenile dispersal did not seem to reflect the preferences revealed during the winter study. In June, preference seemed to be for the semi-open wet areas, but variation within the small sample of animals using the plot suggested that the

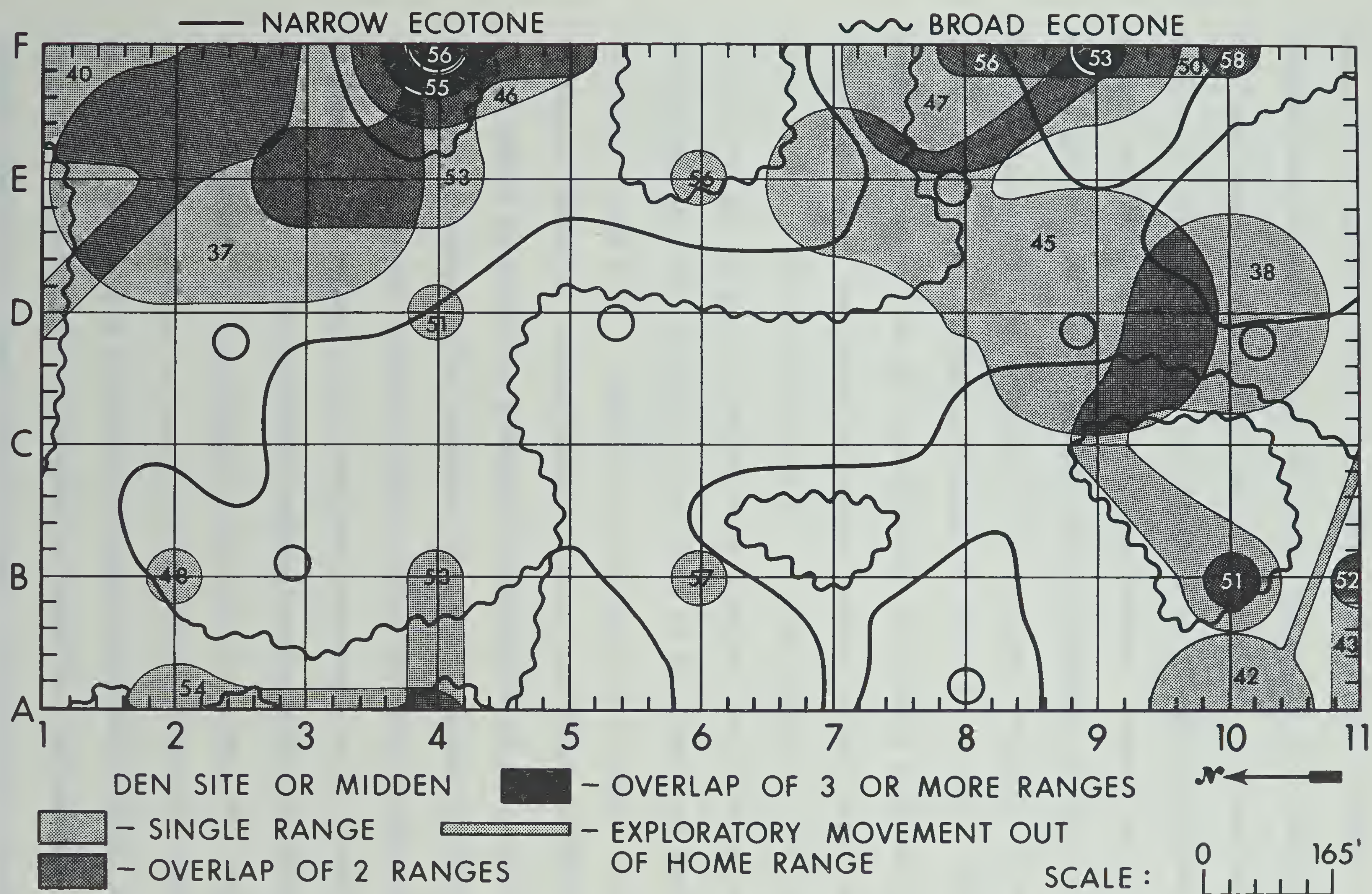


FIGURE 43 . MOVEMENTS AND HOME RANGES
(for Juveniles only) - AUGUST

dense wet areas were equally preferred. There was no longer any tendency to make use of drier habitat as during the spring melt, and both the open and semi-open dry regions were little used. In June, however, this would have been due to the danger from predators in more open forest, rather than to any weather influences. Lowered activity after the mating season, and especially during pregnancy and early lactation in females, was likely the cause of the slight reduction in total area of the plot occupied from May values in the winter study. This was temporary, however, as at the beginning of juvenile dispersal and with the expansion of the ranges of parous females in July there was a great increase in the total area of the plot occupied. The increase in size of the ranges of females with young at that time was apparently responsible for the increase in per cent of semi-open and dense wet landscape types used. Subsequent shrinking of the ranges of adults in August seemed to reverse this, although individual variation, small sample size and the presence of dispersing young partially obscured the change. The greatest changes in habitat utilization occurred in the dry regions, with a sudden doubling of the percentage of each in use during July. This was attributed to an avoidance by transients of more successfully defended areas; areas of good habitat which the mother of a particular litter may have kept for herself, similar areas in which a dominant or preferred juvenile female had successfully set up a territory, or areas occupied by other females. This utilization of poorer habitat by juveniles, and perhaps some adults less able to cope with the sudden rush of young, laster in the winter study to the beginning of cold weather when such areas became uninhabitable and squirrels confined to them likely died.

DISCUSSION

In this section, the biology of *T. h. preblei* is discussed under several headings, and within each, differences from recorded information for more southern subspecies are emphasized in an attempt to identify adaptations to life in the subarctic boreal forest. The outstanding features of the subarctic environment are: a short growing season and therefore limited primary production, long winters with temperature extremes as low as or lower than in the true arctic, snow cover lasting for more than half of the year, snow of a sufficiently low density and fine texture to inhibit movement but provide a highly insulative ground cover, and extreme temperature and humidity changes in the environment of small mammals during the build-up of the snow blanket in fall and its loss in spring.

I. The problem of keeping warm during the severe northern winter

a. Increased body size - Bergmann's rule

Considerable difference was noted in body size between individual red squirrels. Even more variation was evident in body weights, as the weight of stomach contents in an individual could change as much as 15 grams each day. However, statistical treatment made possible a comparison with sizes and weights recorded in other works. A generally larger size, about 11 per cent in body weight (Figure 17) and 4 per cent in standard external and skeletal measurements (Figures 18, 19, 20), was recorded for *T. h. preblei* over *T. h. loquax* (Layne 1954). Nellis' (1969) skull measurements for *T. h. richardsoni* in Montana average mid-way between those for *T. h. loquax* and *T. h. preblei*. This relationship suggests a reduction in the surface area to mass

ratio from south to north. A trend for increasingly northern subspecies of a widely distributed species to increase in body size has been well documented, and its significance may be considered one of many adaptations for survival in cold climates (Schwartz 1963).

b. Avoidance of coldest microclimates

Layne (1954) concluded that adverse weather conditions and lowered temperatures have no long term effect on red squirrel activity in New York, although activity is usually reduced for a few days at the onset of bad weather. Responses to inclement weather are apparently the same for the grey (*Sciurus carolinensis*) and the fox (*S. niger*) squirrel as well (Bakken 1959). In the north, squirrels seem to react similarly in fall when temperatures are near freezing, although this is somewhat obscured by progressively decreasing activity with the coming of winter. It appears that severe mid-winter temperatures elicit a different type of response, namely, retreat to a warmer environment within the snow layers. Squirrels occupy the position between mammals large enough to stay on the snow surface without excessive heat loss, and those which must remain permanently in the warmest microhabitats under an insulative blanket of snow (Scholander *et al.* 1950). This is a rather artificial division, considering only physical mechanisms for thermoregulation, but is an accurate enough generality for mammals of the boreal forest. It must be used with caution for euarctic small mammals where metabolic adaptations are often more important than the obvious physical ones (Schwartz 1963). The importance of snow as an environmental factor has been discussed by Formozov (1946), Pruitt (1957, 1958, 1960, 1970), Coulianos and Johnels (1962) and Fuller (1967, 1969). Pruitt and Lucier (1958)

recorded a relationship similar to that of the present study between red squirrel activity and temperature in Alaska, as did Naumov and Gol'tsmeier (in Ognev 1940) for *Sciurus vulgaris* in Russia. However, mid-winter red squirrel activity has been previously described as subnivean: under the snow at the level of the pukak (Pruitt 1970: depth hoar or ice-latticed space at the snow-ground interface). Squirrels are too large to take advantage of such a narrow space, except in very dense scrub where the snow is held farther from the ground. The present work shows mid-winter squirrel activity to be intranivean: in tunnels through the snow at the level where snow density will support their weight. There is a difference in principle between truly subnivean rodents and the red squirrel, as the latter does not forage beneath the snow (see below, p. 97).

c. Metabolic adaptations to cold stress

An increase in weights of internal organs, reflecting increased metabolism, is expected as a reaction to stresses of low temperature and stress of change in metabolic direction during the northern spring and fall (Schwartz 1963). However, no statistically admissible evidence of such a reaction was recorded in the present work. Some rather tenuous and indirect evidence for response to severe environmental conditions may be obtained from observations of sex differences in organ weights during winter and spring, but these will be discussed with differential mortality under the heading of population dynamics (see below, p. 117, 118).

Brown fat is a high energy storage tissue valuable in non-shivering thermogenesis in small and newborn mammals (Smith and Horwitz 1969). It has been the subject of much research in the past decade, and has

been recorded in adults of all hibernators and several species of non-hibernating small mammals as well. Aleksiuk (1970) reported that although studies on red squirrels in the south had shown no brown fat, it was possessed by red squirrels in Manitoba and presumably those further north as well. This was confirmed by the present study. Physiological studies on laboratory rats (Smith and Roberts 1964) and on the meadow vole (*Microtus pennsylvanicus*) in the field (Didow and Hayward 1969) have shown that brown adipose tissue hypertrophies as the metabolic rate increases during cold acclimation. Therefore, the finding of seasonally high brown fat weights in winter, and low in summer, was expected and is considered as evidence of a significant adaptation to life in the northern environment.

d. Finding sufficient food

It has been recorded that, in winter, red squirrels are not able to move about normally and forage in the treetops due to qali (Pruitt 1958: snow hanging on the branches of trees). During the coldest months of winter, low temperatures combined with the energy expense of floundering over the characteristically soft boreal forest snows prevent movement on the snow surface, except where the ground is almost bare beneath logs or in very dense forests. The possibility of foraging in the warmer, but narrow and icy subnivean space has already been ruled out due to the relatively large size of the red squirrel, and areas of greater space under dense scrub are too infrequent to be of importance. In forests where red squirrels are found, except for some marginal habitat bordering muskeg bogs, there is no spongy moss layer between the subnivean space and the soil as that used by tunnelling arctic rodents (Tikhomirov 1959, Schwartz 1963). These movement-

limiting factors combine to cause a 30-fold contraction in home range size from summer to mid-winter. Winter food caches, characteristic of the red squirrel, are therefore necessary. To reach the caches, permanent intranivean tunnels cut through soft snow on top of the dense and icy older layers, seem to involve less energy expence than the possible alternatives. The tunnels offer a possible additional advantage, especially when small open areas are to be crossed, in allowing squirrels to keep out of sight of the few northern predators.

The necessity of winter food stores, with observations of frequent shifting of home ranges in early winter, together reveal another relationship between red squirrels and the northern environment. A change in center of activity, or the incorporation of a second midden into a squirrel's range just prior to mid-winter restriction of activity, requires that the new owner use food stores made by the previous occupant. The new occupant must be able to find such food even though it was stored by another squirrel and is buried under snow. The problem facing the new occupant is analagous to that facing small birds such as tits (*Parus* spp.). Haftorn (1956) showed that tits store in characteristic places and, in winter, search similar places rather than depending on their "memory" of the precise location of their own caches. Sharp (1959) observed a similar phenomenon in grey squirrels, where several individuals would store food at random over common ground. Haftorn referred to this method of food storing and retrieval as a "communal" system. The territorial nature of the red squirrel forces a more limited action of communal use of food stores, but its value to survival of the population through winter is still unequivocal. It seems evident that only those middens with food

stores from a previous occupant receive attention from potential immigrants during early winter, as demonstrated by the lack of interest in the winter vacancy between traps D-2 and 3 in the present study.

II. Social behavior

a. Territory and home range

Red squirrels in the north were extremely intolerant of each other except during breeding. Smith (1968) noted occasional tolerance between non-breeding adults in southern British Columbia but none was observed in the present work. Layne (1954) reported that red squirrels in New York were almost social, but Smith suggested that this was an artifact and that the natural territoriality had broken down due to interference from the rather gregarious grey squirrel. The social behavior of the latter species has been described by Flyger (1955, 1960), Bakken (1959) and Sharp (1959). Overlaps between home ranges noted for *T. h. preblei* and in Smith's (1968) work represented contested ground, not neutral or common ground as in grey and fox squirrels. Although a greater degree of natural overlap between neighboring ranges was noted in the present work than was recorded by Smith, this could be expected as a consequence of the more difficult defense of peripheral areas when home range sizes become larger in sparse northern populations. In spite of possible minor variations, and the apparent exception due to interspecific competition in New York (Layne 1954), it may be concluded that home range and territory are synonymous in the red squirrel.

Area needed to obtain food did not appear to have any direct bearing on size of home range or territory in this study of red squirrels, excluding that time during which stored food was utilized at maximum restriction of activity. Range of movement then reflected the area over which food was cached. Through November and December, when home range sizes were much reduced, squirrels were not only feeding normally but also still gathering food for winter. At their largest, the sizes of individual ranges seemed generally indicative of the amount of available space over a large and discontinuous area of suitable habitat, with local differences arising from competition for preferred areas. This is in contrast to the situation in southern British Colubmia (Smith 1968), where population densities were very high and apparently limited by food supply rather than by the effect of weather on a limited number of suitable winter microhabitats. Territory sizes in Smith's study area were also apparently determined by food supply.

Frequent shifting of squirrel home ranges was noted by Layne (1954) and considered to be a response to better food supplies. However, a number of factors apparently were involved in the changes in centers of activity and areas of home range observed in this study. Moves commonly occurred after the death of a resident squirrel created a vacancy. Vacancies in early and late winter were immediately filled when (1) the number of squirrels and amount of overlap of home ranges was large, and (2) the quality of the available areas was high in terms of food and shelter. A few moves occurred well after a vacancy was formed, or without a pre-existing vacancy, apparently due to social conflict between neighbors. The tendency for changes in

areas of home range to occur was closely correlated with seasonal changes in behavior. A fall or early winter reshuffle of home ranges apparently occurs when squirrels are seeking, or actively competing for productive and sheltered areas of large size in which to endure the winter (Figures 32, 33). This phenomenon has been observed, but not satisfactorily explained, by workers on the grey and fox squirrels of the northeastern United States (Flyger 1960). During spring, shifts in home ranges of females were rather rare (Figures 37, 38). When noted they were apparently due to social conflict with more aggressive adults successfully expanding their ranges after winter restriction, or to having been chased out of areas of familiarity by breeding males. Shifting of home ranges during spring was almost entirely limited to males, as evidenced by the influx of new squirrels onto the study plot in April and May (Figures 37, 38). Flyger (1960) attributed a parallel observation in the grey squirrel to males becoming lost in their long range wanderings in search and in pursuit of breeding females. The same conclusion was drawn in the present study.

It was observed during the winter months, except January when temperatures were usually colder than -20°F., that newly vacant middens in sheltered, productive areas were immediately occupied by a new squirrel. Similar results were recorded by Smith (1968) who emphasized the rapidity of such replacement. This suggests some mechanism for social contact between squirrels which may occupy ranges some distance apart, even when the boundaries of neighboring home ranges have separated from each other during increasingly cold weather. It is likely that sporadic movement serves an important function in this regard, as such movement was usually observed just prior to shifts in

area of occupancy. Further, as most sporadic movement occurred in late winter or spring, when it apparently was responsible for the capture of 11 previously unrecorded males and 3 females, it may be that its action as a mechanism of contact or communication is of considerable importance in co-ordination of breeding (Smith 1968). Spring was also the season when boundaries between squirrels were being re-established after winter isolation. This may have further increased sporadic movement, as such movement was especially common prior to shifts when crowding was evident.

Previous authors have reported that the home ranges of adult male squirrels are of larger size than those of adult females (Layne 1954). In this study, sufficiently accurate and numerous observations to show any definite relationship could not be obtained during fall, winter or early spring, when extreme variability seemed to be the rule. Relative aggressiveness of individuals, determining the results of dominant-subordinate interactions, was apparently the major factor influencing home range size. This was demonstrated by the relatively large areas controlled during winter and spring by male No. 5 and females No. 15 and 16 (Figures 33 to 38), apparently the most aggressive squirrels on the study plot or in its vicinity. Presumably, these animals were benefiting from increased food supply and avialability of shelter at more than one location. During spring breeding, the intense activity of males in contrast to the rather sedentary nature of females may have resulted in a corresponding increase in home range size. However, as most of such activity was in the form of sporadic movement which must be excluded from calculations estimating home range (Burt 1943), no difference in home range size between the sexes

was noted. During early summer, females may show contracted home ranges as a reaction to the period of parturition, and later to maternal care during lactation. A marked expansion of the home ranges of parous females and, immediately following, a contraction to sizes again similar to those of males and nulliparous females was noted later in summer (see below, p. 105).

Taylor (1966) reported that young grey squirrels were subordinate to older ones. If this relationship also applies to red squirrels, it would be expected to show in smaller home ranges for younger squirrels. Such a situation was evident from live-trapping records for juveniles during early dispersal. However, with the highly territorial nature of red squirrels in this study, social position after that time seemed to depend more on ownership of an established range than on age *per se*. Smith (1968) reported that young red squirrels had difficulty establishing ranges at high population densities in southern British Columbia. However, likely due to the much more sparse populations recorded in this than in red squirrel studies to the south, a number of young red squirrels on the plot in the fall of 1968 did become rapidly established, and some ended with larger ranges than resident adults (eg. Nos. 5, 3, 14, 16 Figure 31).

The aforementioned age, sex and seasonal differences in territoriality are mirrored by changes in the relative weight of red squirrel anal glands. There has been little previous work concerning the function of this organ. Layne (1954) speculated that it may serve in females as a scent gland for attraction and reproductive synchronization of males during the breeding season. However, Smith (1968) suggested that this function is carried out by vaginal secretions present in

copious quantities during estrus. Evidence in the present study supports the latter hypothesis. It is suggested here that the function of the anal gland is as a territory marker operating through odor deposit on the feces. Changes in anal gland weights were: growth in juveniles until the acquisiton of a territorial instinct; increased weight in summer and fall associated with more numerous territorial conflicts during warm weather and juvenile dispersal; greater weights for male than female squirrels in spring, reflecting the intense breeding activity of males; and greater weight for females than males during summer, reflecting the intense territoriality of maternal behavior. In fall, females apparently do not begin storing food until after weaning the young, well after adult males have started their winter caches (Smith 1968). Increased weights of anal glands in females over males in fall might therefore be expected with increased activity necessary to create food stores in the short time available before winter, but differences in the data were not statistically significant. Finally, the heavier anal glands recorded for males than for females during winter may be evidence for greater activity of males, although sample size is too small for such evidence to be statistically admissible. The relationships shown between anal gland weights and red squirrel activity seem to reflect differences in home range size. Exceptions occur when the territorial behavior of males conflicts with the apparent partial abandonment of territories and encounter of new areas during the extreme activity of breeding; and when parous females are showing extreme activity to satisfy the food requirements of lactation but are not ranging far from the nest site. The evidence suggests than anal gland secretion

is in direct relation to the incidence of social interactions, taking into account the extremely territorial nature of the red squirrel.

Territoriality serves to prevent over-exploitation of suitable habitat (Wynne-Edwards 1962, Eibl-Eibesfeldt 1970), thereby stabilizing populations at densities near the carrying capacity of the environment. Therefore, the adaptive significance of the increased territorial nature of red squirrels in the north is to increase stability as population size becomes critical with diminishing carrying capacity.

b. Maternal behavior

Taylor's (1966) work on the grey squirrel in England, and similar studies on the Eurasian red squirrel (Ognev 1940), show a consolidation or slight reduction in the size of home ranges of females in late pregnancy and during lactation. Layne (1954) suggested a similar phenomenon may have been present in the red squirrel, and the results of the present study (Figures 38, 39) seem to confirm it. Smith (1968) reported that activity was actually greater during lactation due to increased energy requirements and more time spent feeding, but showed that this activity was confined to the nest area. A great increase in the area defended by females with young during weaning and the early stages of juvenile dispersal has apparently not been previously described, but it is likely that no such expansion could occur in such dense populations as those described by Smith (1968) in southern British Columbia. However, both studies show that young red squirrels disperse into unoccupied areas at the edge of their mother's territory, or in an area of her range from which she has withdrawn. The justification of range expansion, where possible, may be to ensure

the establishement of at least some of the young without dangerous energy loss through reduction in the adult female's feeding range. It would seem to be of greater value in populations of low density, and may explain the movement of squirrel No. 1 in this study to a less crowded area off the study plot just prior to weaning her young. Smith (1968) reported that the young are usually moved to a temporary nest at the boundary of their mother's territory just before weaning, but unless this was true of female No. 14, it was not recorded in this study and young dispersed from the nest in which they were born. Such a movement may not be important in a relatively sparse population such as that described in the present work, where large enough undefended areas are available during the period of dispersion that conflict for the area retained by the adult is avoided. There is total agreement between Smith's and the present work concerning the description of dispersion *per se*, with the adult female keeping the best section of the defended area for herself, the most productive and largest parts of what is left going to the dominant female in the litter, and the rest competed for by the remaining females. Young males are almost all immediately forced from the home area, and become transients in search of unoccupied regions (Figure 43). Smith suggested that participation in sex play, found only in young males after weaning was completed, resulted in their subordinate position through the associated appeasing calls. This behavior seems to protect juvenile males from aggression when trespassing on the territories of strange adults, although not from their mother or female littermates, and may be important in ensuring that they find enough food for a short time until such behavior ceases. The adaptive

significance of such preferential treatment of female young would appear to be in increasing the source of the following year's recruitment, in a species with promiscuous males.

c. Social stress and endocrine function

If relative adrenal weight in red squirrels is a reliable indicator of epinephrine production, it follows that age, sex and seasonal differences evidenced in the present study were in response to corresponding variation in physiological stresses. The few significant changes recorded all seemed to be in response to stress from social interactions, which are probably more intense in the highly territorial northern populations than in the less territorial southern ones. However, no previous studies of the red squirrel have yielded similar data for comparison.

Adrenal weights in juveniles are highest, evidence for increased social stress, during early dispersal - directly after leaving the mother's care and encountering territorial aggression for the first time. It was expected, and observed, that adrenal weights were higher in young males than females in the earliest records (Figure 21). This difference was no longer evident after about 100 days of age, the age at which females were no longer tolerated on their mother's territory (Smith 1968). These observations are in agreement with hypotheses concerning social status and territory size in young red squirrels presented in this and Smith's study. Although no significant differences were seen in home range sizes after that time, higher adrenal weights for juveniles between the ages of 140 days and one year than for older squirrels may support Taylor's (1966) suggestion of a generally lower status of juveniles. Thiessen (1966) showed

that social status and activity were related in *Mus musculus*. He suggested that such a relationship was important in maintenance of population size, as young males were likely to migrate away from densely populated areas. The same phenomenon seems also to be important in populations of the red squirrel.

It is well known that in many species of small mammals, increases in population density bring about increasing stress from social interaction - evidenced by heightened adrenal activity (Thiessen and Rodgers 1961). This relationship was especially evident in the north, apparently due to the marked territoriality of red squirrels. The density-stress-adrenal hypertrophy cycle apparently occurs with two general modifications in two different groups of rodent species The difference between them seems to be that rodents of the first group are permanently in breeding condition whereas those of the second group show a marked seasonal development and regression of the gonads. In the former category are such species as *Mus musculus* (Christian and Davis 1966), *Microtus pennsylvanicus* and *M. montanus* (McKeever 1959, Christian and Davis 1964, 1966), and *Rattus norvegicus* (Christian 1967), which show a great increase in adrenal weight for females and a slight decrease for males at sexual maturity. This level is maintained with no further variation through changes in reproductive condition, and the adrenal weight cycle in adults is apparently due entirely to seasonal population differences. In species of the second category, and perhaps occasionally of the first group under different environmental conditions, a different pattern is evident at maturity. *Sigmodon hispidus* (Goertz 1965), *Marmota monax* (Christian 1962), *Microtus agrestis* (Chitty 1961, Chitty and

Clarke 1963), *Peromyscus* sp. (Christian 1967) and *Eutamias* sp. (Sheppard 1968) show no permanent change in adrenal weight at sexual maturity, and apparently respond to both population density and reproductive condition on a seasonal cycle. Males usually respond much less to reproductive condition than do females. The red squirrel falls into this category.

In the present study, the spring increase in adrenal weight observed with sexual development and breeding was attributed partly also to a marked increase in activity with warming temperatures. Females of species in the second category commonly show heavier adrenals than males at this time, even though they may be less aggressive, indicating the presence of a marked adrenal response to pregnancy. In red squirrels, although adult males may show equal or slightly greater adrenal weights than adult females, their intense breeding activity compared to males of other species can account for the disagreement. An adrenal response, presumably to pregnancy, was still noted in females. The greater adrenal response in yearlings than in adults at this time, particularly in females (where adrenal weights do exceed those of males), may be attributed to "physiological inexperience" (Sadleir 1969).

The occurrence of peak adrenal weights in summer, the season of peak activity and population size, is common to most species of rodents. *Citellus* sp. (McKeever 1963, 1964) are exceptions, with the peak weights occurring in spring. These exceptions are expected, however, in social rodents where population density is not normally a source of stress. Significantly heavier adrenals in female than male red squirrels during summer may be attributed to the added stresses of

lactation and early post-weaning care on the female. During fall, stresses from increased population density and increased activity in preparation of food stores for winter (Sheppard 1968) were apparently equal for both sexes and not significantly different from the stresses of spring. Although sample size is very small, low adrenal weights observed during the reduced activity of winter are in agreement with the social stress hypothesis, as this is a time of marked decrease in social conflict.

III. Changes in timing of biological cycles due to changes in timing and duration of seasons

a. Pelage changes

The molt sequence recorded for *T. h. preblei* seems to agree closely with Layne's (1954) description for *T. h. loquax* in New York, except for timing differences and the nature of the change from juvenile pelage. The latter was not a true molt as suggested in Layne's work, and the description more closely coincides with that for the Eurasian red squirrel (*Sciurus vulgaris*) given by Russian authors (Ognev 1940) in which there is growth of new hair without loss of old hair.

The fall molt in the north began about a week earlier than was recorded by Layne and ended about four weeks earlier, which means that it took place much more rapidly. This could more-or-less be expected with differences in the timing, duration and intensity of seasons between north and south. Regarding the spring molt, it is well known that, as a rule, the periods of molting and the bearing of young are chronologically separated in mammals to prevent the high energy demands of these processes from becoming additive. However, in the

north, the shortness of the warm season necessary for birth and dispersal of the single litter of young necessitates the coincidence of pregnancy, lactation and molting in many forms (Schwartz 1963). In the present study only pregnancy and molt were made to overlap, with lactation occurring in the warmer and usually productive summer. The consequence of energy demands of pregnancy and molt occurring together and during the social and environmental stress of spring in the north may be as a factor increasing spring mortality and decreasing breeding success. An apparent paradox was observed in the present study, as the spring molt seemed to begin earlier and was complete about three weeks earlier than the south. This is exactly opposite to the expected sequence due to the longer and colder winters in the north. A tentative explanation may be obtained from the observation that, in Layne's study, the spring molt in females occurred slightly later than in males and during the period of lactation between the two breeding seasons. The validity of the above explanation of apparently delayed spring molt for *T. h. loquax* therefore lies in speculation that energy demands while females are lactating are less than those during pregnancy. This is possible, even though lactation *per se* demands more energy than pregnancy as: 1) much of the increased metabolism during lactation, as revealed by adrenal weights, is apparently due to stresses from increasing population density; 2) *T. h. loquax* is a rather social subspecies so individuals are probably not subjected to these stresses; and 3) squirrels in New York are still stressed in spring by the aggressive breeding behavior of males. Therefore, the possibility exists that the period of molt is of less metabolic consequence to southern squirrels when occurring during lactation. A further possibility is that any increased energy

demands during pregnancy may act to decrease fecundity, and are therefore avoided where possible.

b. Gross seasonal changes in the reproductive tract

Anatomical changes on the gross and cellular levels during the reproductive cycle of the red squirrel have been thoroughly described and discussed by Millar (1968). Changes seen during the present study were identical with those outlined by Millar except that he failed to note the brief vaginal bloodiness occurring just after copulation and the traces of vaginal coiling in very young females. Timing and duration of some phases of the reproductive cycle were different from those reported in previous works, apparently due to the more northerly location of the study area. Discussion in this section will be limited to such differences.

Initiation of gonadal development in male red squirrels occurs about two weeks earlier in New York (Layne 1954), and a few days earlier in southern British Columbia (Millar 1968, 1970), than was recorded in this study. Spring breeding occurs in January in New York and, although dates are variable, usually March in southern British Columbia according to the same authors. It occurred from late April to early May in the north in 1969 and about three weeks earlier in 1968. This geographic progression suggests that the attainment of breeding condition occurs progressively later in the year with habitat change from the eastern deciduous forests to the western conifer belt (Millar 1968, 1970), and with latitude from south to north. This appears to affect females more than males, as there was little difference noted in the timing of initiation of male sexual development between the three locations and significant difference in the timing for females, especially

between New York and the area of this study. Evidence for control of timing of breeding by weather, as suggested for red squirrels by Millar (1968, 1970), was seen in differences recorded between the 1968 and 1969 breeding seasons in this study. The relatively mild winter and long spring of 1968, as opposed to the cold winter and relatively sudden, early, wet spring in 1969, may account for the apparent four to six weeks difference in the timing of the breeding seasons noted between the two years. In 1968, the young were born while the weather was still cold, but they dispersed during the warm, dry period of the following fruiting season. In 1969, the young were born during a comparatively cold, wet summer with a later and poorer fruiting season, and were still dispersing at the beginning of the cold period in September. It is interesting to note that two yearling females taken at the Mackenzie River Crossing were already lactating on May 24, 1969 - i.e. three weeks earlier than those in the sample collected within the study area. The crossing is 60 miles west of the study area, and had a warmer winter with less snow and an early but dry spring, likely due to the moderating effect of the nearby river. This is further evidence supporting Millar's (1968, 1970) hypothesis. Schwartz (1963), in discussing the breeding phenology of boreal and tundra mammals, suggested that dependence on the coming of spring weather for breeding is important in determining the northern limit of a species - the latitude at which the period available for recruitment is no longer sufficient to allow a balance with mortality. Records taken during the present study suggest that even an early reproductive season, as occurred in 1968, barely allows enough time for juveniles to disperse and prepare for winter. The importance of small areas with climates moderated by

large water bodies as red squirrels approach their northern limit is therefore demonstrated.

It was noted that, during the late breeding season of 1969, testes apparently reached peak weights some three weeks before females entered estrus and before the other male organs reached maximum size, rather than the expected close synchrony in peak development of all organs reported by Millar (1968, 1970). It is suggested that, in the north, breeding usually occurs in late March and April as was noted in 1968, and the attainment of peak breeding condition is usually synchronous in all organs between the sexes. It is further suggested in this work that the time of initiation of breeding is determined by the female, possibly through an increased physiological sensitivity to weather and habitat-food conditions. Sexual development usually begins earlier in males than in females (Layne 1954, Millar 1968, 1970), and timing of peak male development is apparently under control of some pheromone present with the desquamated cells in the coiled vagina of the estrous female (Smith 1968). Millar's (1968, 1970) data showing response of the male sex tract to be more rapid with earlier female development and more intense with a larger percentage of females breeding may be interpreted to support such a hypothesis.

IV. Population dynamics

a. Mortality

Naumov and others (in Ognev 1940) suggest that squirrels of the Eurasian genus *Sciurus* live to 8 or 9 or even 12 years of age, although most other workers have given 5 years as the maximum age (Ognev 1940, Lampio 1965, 1967). The disagreement with Naumov's findings on aging

seems to have arisen from his interpretation of observations of tooth wear. Tooth wear classes for aging used in this study were developed independently, but later found to correspond closely with those described by Nellis (1969) in Montana. His work and that of Layne (1954), suggest that *Tamiasciurus hudsonicus* may live to 5 or 6 years at more southern latitudes, a year or two longer than was found in the present study. If, as suspected, the wearing out of the molar teeth is the direct cause of death at "old age", such a discrepancy with latitude could be explained as a result of the higher metabolic rate and need for a higher food intake in more northerly squirrels.

Factors influencing red squirrel mortality, and therefore, mortality rate, may be expected to vary seasonally. The coming of cold weather in fall acts to limit the population to those animals which have been able to find, defend and prepare habitats suitable for winter. The length, suddenness and severity of the fall season may therefore be important in determining the number of young squirrels which are able to effectively disperse before the habitats in which they disperse are rendered uninhabitable by cold weather. As these factors act mainly on the juvenile cohort, time, as well as the number of suitable habitats, seems to be a major limiting factor. More rapid growth and earlier maturity than in southern forms would therefore be of adaptive advantage. Although the estimate of gestation time in this study agrees with the 41 days given for red squirrels in the literature (Layne 1954, Millar 1968), there is a slight disagreement concerning the duration of lactation, previously given as about 51 days. In this study, the total period from the record of the first lactating adult to that of the last lactating yearling was 52 days. However, when adult and

juvenile cohorts in the sample are separated, the lactation periods revealed in the collected sample appeared as 36 and 38 days respectively. There was a period preceding and following parturition when no females were taken (Smith 1968, this study). An estimate of duration of lactation from the results of this work, taking into account the 12-day haitus in each class when females were not collected, would be about 45 days. Either northern squirrels are weaned earlier or Layne's (1954) estimate, based on observations from a hand-reared litter, is of exaggerated length. Millar's (1968) results, which are in agreement with Layne's, did not consider the effect of separating age classes. The 45-day estimate coincides with the lactation period observed for *Sciurus vulgaris* in Russia (Ognev 1940) and with the time of appearance of young with known birth-dates in live traps on the study plot. In addition to these rather tenuous data suggesting rapid early development, it is evident from autopsy data on dispersing juveniles that northern squirrels grow slightly faster after weaning than those in New York (Layne 1954). The difference in rates of development between the subspecies is approximately 20 per cent. (Observations on a litter of nestlings during an unsuccessful attempt to rear them by hand also seem to support this value, especially with reference to the comprehensive description of development given by Layne (1954).) *T. h. preblei* in the north has therefore adapted through an accelerated growth rate to the short period of warm weather between birth and the extreme northern winter. It should also be noted that, because females appear to grow slightly faster than males, and because females are favored in the establishment of territories at dispersal (Figures 41, 43), mortality at the onset of cold weather is probably greater in young

males than young females. However, no other indications of such an early divergence in the sex ratio was noted.

Winter mortality of squirrels that were successfully established in the fall was apparently low. Although not statistically significant, higher weights during winter of adrenals, kidney, spleen and brown fat in females than males suggest a greater metabolic response to cold and perhaps therefore a higher survival rate for females. A slightly lower or more variable liver weight in females than males is consistent with the hypothesis of a greater metabolic demand in females coinciding with winter food shortage. Heavier anal glands in males than females at this time suggest that territorial behavior may be greater in males. This, in winter, would act to further increase male mortality.

Mortality seemed to increase again in spring, perhaps due to the coincidence of the energy demands of breeding and molt with harsh conditions in the environment. The fall decrease and March increase in activity and home range size appear directly related to temperature. The sudden nature of these changes may be related to the spring and fall thermal overturns described by Pruitt (1957), and may account for the slight increase in kidney weight during these seasons (Schwartz 1963). The correlation between temperature and activity according to trap records breaks down in late April and early May when the snow cover is melting. A greater number of hours per day produced home ranges that were larger than in March, but trap success per hour was considerably less. Much of the increased activity of breeding was observed to take place in the treetops where the animals were not exposed to traps. This was apparently a response to the inundated condition of the ground and the occurrence of "spring snow" which is

crusted at night and soft and wet by day. However, as actual mating chases take place mostly on the ground, squirrels, like other northern small mammals, may be subjected to a spring critical period (Fuller 1969). Notes attesting to the generally poor physical condition of squirrels during breeding seem to verify this hypothesis. It also appears, from the sexual difference noted in breeding activity, that mortality due to effects of the spring critical period was greater among males than females. During spring, kidney weights were significantly greater than those recorded during summer in males but not in females (Figure 22), spleen weights of males were significantly greater than those of females (Figure 24), and weights of adrenals and liver were slightly greater in males than females (Figures 21, 23). Heavier organ weights in males than in females, attesting to a higher metabolic rate (coinciding with food abundance) in males (Schwartz 1963) were also noted during fall. Conflicting evidence was recorded during summer, with weights of adrenals, kidneys and liver greater in females than males, and spleen weights showing the opposite relationship. This was apparently due to a temporary increase in the metabolic rate of females during lactation. However, a generally higher metabolic rate for males is in agreement with the hypothesis of Taber and Dasman (1954). A generally higher metabolic rate, with consequently greater food intake and more rapid wearing of the teeth, would be expected to reduce the life span in the male. All the aforementioned factors then, and especially those acting during the breeding season, contribute to reversing the slight bias in favor of males in the sex ratio at birth (also noted for red squirrels in Layne's (1954) work) to produce a preponderance of females in the oldest age groups (Lampio 1965, 1967).

b. Natality

Red squirrels in the Northwest Territories have only one breeding season each year, as previously noted by Wood (1967) in Wood Buffalo National Park. However, there is some potential for variation in the species. Millar (1968, 1970) and Smith (1968) have noted that one breeding season is usual for *T. h. languinosis*, *T. h. streatori* and *T. douglassi* in southern British Columbia, although rarely a second litter occurs. Two litters per year are the rule for *T. h. loquax* in New York. In the U.S.S.R., *Sciurus vulgaris* commonly has three litters each year in the south, two in central Russia and one in the northern parts of its range (Ognev 1940). This progression is directly related to length and apparent quality of the season available for juvenile care and dispersal. Although there is little difference in latitude between New York and southern British Columbia, and although the climate is more severe in the east, the amount of food produced in the eastern deciduous forest and the length of time it is available is apparently greater than in the western coniferous regions. It would seem worth while to obtain and study comparative data for squirrels in the deciduous forest regions of southern Manitoba, where similar tree cover occurs but the climate is much more severe than in New York.

Layne (1954) reported a mean litter size of 4.5 in New York, whereas the overall mean for this study was 3.7 (4.0 in 1968 and 3.4 in 1969). These data are a direct conflict with Lord's (1960) hypothesis that a positive correlation exists between litter size and latitude in tree squirrels.

Differences in productivity observed for 1968 and 1969 were correlated with differences in weather recorded for the two years.

Smith (1965) and Millar (1968) suggest that, in southern British Columbia, reduced fecundity can arise through a poor spring food supply. Both found a higher level of productivity in red squirrels that fed all winter on stored lodgepole pine (*Pinus contorta*) cones, than in those that depended on Douglas fir (*Psuedotsuga menziesii*). In the areas where squirrels were collected for this study, the predominant food species were jackpine (*Pinus banksiana*) and spruce (*Picea glauca* and *P. mariana*). These species present many of the same characteristics to a squirrel as those discussed by Millar. Pine produces stable cone crops, and the cones remain on the trees for many months - not normally opening to release their seeds. Spruce cone production varies widely from year to year and although the cones are easily opened and seeds are of initially higher energy, the cones open and release their seeds when mature. In this study, there appeared to be higher squirrel populations in areas of pine forests than in areas of spruce, indicating that Millar's (1968) hypothesis may be applicable. However, although no quantitative estimates of cone crops were recorded, no large differences in cone production were noted between the two years and it seems unlikely that any minor differences could be enough to bring about as much of a change in fecundity as was noted in this study. Further, there were differences in weather conditions between spring 1968 and 1969. These had a profound effect on the environment. During the 1969 breeding period, although a good food supply in the form of conifer buds, pre-cut cones and overwintered berries was available, there was as much as four inches of water on the ground and squirrels seemed to fare poorly in the constant wet and cold. The cold winter *per se* did not noticeably affect squirrel populations, but the early and very

wet spring apparently did. Breeding success was noticeably lower, and the season so much later in 1969 that many of the young born in that year may not have survived through fall. The implication is that weather exerts a very great effect on recruitment in small mammal populations at northern latitudes (Fuller 1969).

If mortality is higher in the northern boreal forest than in the south, and if fecundity is lower, there must be some compensating factors that permit squirrel populations to maintain themselves in northern regions. One of these differences may be a divergence in the sex ratio, which results in significantly fewer breeding males than females in the population. Thus, given male promiscuity, high breeding efficiency can be maintained by fewer animals. Lampio (1965, 1967) demonstrated that an unbalanced sex ratio is present in the genus *Sciurus* in Finland. The data from the present work suggest a similarly distorted sex ratio, and although these data may be biased because the generally more active males had a greater liklihood of being collected than did the less active females, such a bias would select against the trend recorded.

The major difference in natality between squirrels in the present study and those further south seems to be in the percentage of females in the population which breed. Evidence from Layne (1954) and Millar (1968, 1970) show that females are not normally sexually mature by their first breeding season, and that many adult females often fail to breed as well. No non-breeding adult females were encountered in the present work, and all rising yearling females in this study had reach sexual maturity. The latter observation was apparently due in part to faster growth, and in part to length of time available between breeding

seasons - longer in the north than at the latitude, for instance, of New York. The age at reproductive maturity given in the literature for red squirrels is 7 to 8 months (Millar 1968), whereas all the females collected in this study had reached 10 months of age before their first breeding season. A difference in time required for sexual development between adults and juveniles was recorded. Sexual development in juvenile males began about 10 days later than in adults but apparently caught up during the long period of readiness prior to females entering estrus. In females, juvenile sexual development also began about 10 days later than in adults but this difference was retained throughout the breeding season due to the rapidity of female sexual development after initiation.

Millar (1968) reported no significantly lower productivity in yearling females compared to adults, although he suggested that some differences may have been present. In this study, productivity was noticeably reduced in yearlings relative to older females. Both lowered ovulation rates and increased prenatal mortality apparently are common in yearlings of other sciurids (Sheppard 1969), therefore a similar phenomenon could be expected in the red squirrel. Sadleir (1969) used the term "physiological inexperience" to explain the greater evidence of stress observed in females experiencing their first mating season, and the resulting smaller litter sizes in that group. As a stress acting solely on yearling females, it was likely also important in cases of complete reproductive failure observed in the present work. Data showing adrenal weights to be greater during spring in yearling females than in adults (Figure 21) are in agreement with this explanation. A correlation between stress, increased adrenal activity

and reduced fecundity has been already well documented (Christian and LeMunyan 1958, Thiessen and Rodgers 1961). In the north, social stress during breeding may also be important in reducing fecundity of yearling females. Terman (1969) recorded a higher incidence of complete reproductive failure in yearling than in adult deer mice exposed to social stresses. In the north, the suddenness of the change from comparative isolation of individuals during winter to intense breeding activity and the breakdown of territorial stability at the onset of warming weather may result in more stress than is present in southern populations at that time. An intensified "behavior inexperience" with mating in the north may therefore partly account for the lack of previous records of a stress-fecundity relationship in red squirrels. Although fecundity in yearlings is less than that of adults, natality is increased overall through the increased percentage of females breeding and this is apparently sufficient to offset the high northern mortality.

High rates of natality and extreme year to year variation in reproductive success are characteristic of northern populations (Schwartz 1963). Causes of this variation are still unknown, but the many correlations with weather conditions during the periods of breeding and dispersal of the young cannot safely be ingnored by students of population fluctuation.

CONCLUDING DISCUSSION

Results of this study suggest the following picture of the ecology of the red squirrel in the southern Northwest Territories:

A generally larger size, about 11 per cent in body weight and 4 per cent in standard external measurements was recorded for *T. h. preblei* over *T. h. loquax* in New York (Layne 1954). *T. h. richardsoni* in Montana seems to be about mid-way in size between these two. This progression follows Bergmann's rule for increased size with latitude and may be considered an adaptation for reduced heat loss in a cold climate.

During extremely cold weather, the coldest microclimates were avoided. Squirrels reached their food stores, which are of increased importance in the north, by means of tunnels through the snow at the level of the older, icy layers.

Brown fat weights reflect the importance of this tissue in metabolic adaptations to cold stress. Highest weights were recorded in winter and lowest in summer. This tissue is apparently not present in red squirrels in the southern parts of their range.

Squirrels in the north were extremely intolerant of each other except during breeding. The intensity of territoriality is apparently much greater than in the south, as an adaptation for increasing population stability. Even with this however, a system of "communal food stores" is evident when shifts of home range are made. This system seems of great importance in ensuring that the death of a squirrel prior to the mid-winter restriction of activity does not mean the loss of that animal's food stores to the population, and a transient which might otherwise not survive the winter can find and make use of that food.

Weights of red squirrel anal glands were found to vary directly with seasonal differences in social conflict - with apparent population density. It is suggested that their function is as a territory marker through odor deposit on the feces.

Maternal behavior was found to be definitely biased toward one or more female young in the litter. These more aggressive individuals were usually assisted in establishing and defending a territory at the expense of their male littermates. It is suggested that this is an adaptation to increase the female cohort of the population, thereby increasing the reproductive potential of a population in which males are promiscuous. This phenomenon is present but seems less marked in southern British Columbia (Smith 1968), and was not recorded by Layne (1954) in New York.

Squirrels in the north live to a maximum of four years. Layne (1954) and Nellis (1969) suggest that the maximum age for squirrels in the northern United States is five or six years. Increased mortality in the north is to be expected with the harsh climate. Male red squirrels apparently show a higher mortality than females, again acting to increase the percentage of females in the population. Most of this increased mortality occurred as a result of the intense breeding activity of males, in contrast to the rather sedentary nature of females, during the spring critical period. There was also some evidence of a higher metabolic rate in males, as organ weights were heavier through most of the year. Increased food intake would cause the molar teeth to wear faster, resulting in an earlier death. Exceptions occurred when females were lactating and possibly also in winter, when females may have shown a stronger metabolic response to

cold stress even though anal gland weights suggest males were more active. This latter would be of further survival advantage to females.

Breeding in the north was four months later in the year than in New York (Layne 1954) and somewhat later than in southern British Columbia (Millar 1968) as well, although the dates seemed rather variable. Timing of breeding was apparently determined by the female through a sensitivity to weather conditions. Male peak development seemed to be under pheromone control from secretions of the coiled vagina of the estrus female. Timing of the breeding season was critical in the north, in order to take maximum advantage of the short warm season available for weaning and dispersal of the young.

An increased growth rate was noted in the northern red squirrel. This was important in attaining physical maturity during the short warm season before winter.

Only one litter per year was possible in the north, compared to two in New York (Layne 1954) and sometimes in southern British Columbia as well (Millar 1968). Litter size seems also to decrease with latitude - recorded as 4.5 young per female in New York (Layne 1954), against 3.7 in the north. However, a great increase in the percentage of females breeding, even though fecundity of yearlings was relatively low due to reproductive inexperience, apparently increased natality sufficiently to balance the high northern mortality.

In summary, it may be concluded that the northern subspecies of red squirrels *T. h. preblei* differs from its southern relatives in a number of ways that seem to represent adaptations for coping with the harsh subarctic climate.

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